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Diversifying crop rotations with temporary grasslands : potentials for weed mangement and farmland biodiversity

Helmut Meiss

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Thèse de doctorat nouveau régime - cotutelle
Binationales Promotionsverfahren

Diversifying crop rotations with temporary grasslands:

potentials for weed management and farmland biodiversity

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Institut für Landschaftsökologie und Ressourcenmanagement

Professur für Landschaftsökologie und Landschaftsplanung
Heinrich-Buff-Ring 26-32, D-35392 Gießen, Deutschland

Presentée par : *Vorgelegt von:*
Helmut MEISS

Directeur de thèse (France) : *Betreuer (Frankreich)*:
Prof. Dr. Jacques CANEILL

Co-directeur de thèse (France) : *Ko-Betreuer (Frankreich)*:
Dr. Nicolas MUNIER-JOLAIN

Directeur de thèse (Allemagne) : *Betreuer (Deutschland)*:
Prof. Dr. Rainer WALDHARDT

Date de soutenance : *Tag der Disputation*:
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Jury : ***Prüfungskommission*:**

Dr. François BRETAGNOLLE	Prof.	Université de Bourgogne	Président	*Vorsitz*
Dr. Philippe DEBAEKE	DR	INRA Toulouse	Rapporteur	*Gutachter*
Dr. Bernd HONERMEIER	Prof.	Universität Gießen	Rapporteur	*Gutachter*
Dr. Vincent BRETAGNOLLE	DR	CNRS Chizé	Examinateur	*Beisitzer*
Dr. Bärbel GEROWITT	Prof.	Universität Rostock	Examinatrice	*Beisitzerin*
Dr. Nicolas MUNIER-JOLAIN	IR	INRA Dijon	Encadrant	*Betreuer*
Dr. Rainer WALDHARDT	Prof.	Universität Gießen	Encadrant	*Betreuer*

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ABBREVIATIONS

ANOSIM	Analysis of similarities
ANOVA	Analysis of variance
CAP	Common Agricultural Policy (EU)
CDA	Canonical Discriminant Analysis
DCA	Detrended Correspondence Analysis
FG	Functional Group
ISA	Indicator Species Analysis
IV	Indicator Value
IWM	Integrated Weed Management
MRPP	Multiple Response Permutation Procedure
OSFs	Overwinter Stubble Fields
PFCs	Perennial Forage Crops
SE	Standard Error
SD	Standard Deviation

ABSTRACTS (ENGLISH, FRENCH & GERMAN)

LONG VERSIONS (ABOUT 1500 WORDS)

Extended summary in English

Diversifying crop rotations with temporary grasslands: potentials for combining weed management and the conservation of biodiversity

In spite of more than 60 years of agricultural intensification and a massive use of herbicides in industrialized countries, arable weeds continue to be a serious threat to agricultural production. At the same time, the dramatic loss of biodiversity in farmed landscapes, environmental pollution, high economic costs of herbicides and the increasing selection of herbicide resistant weeds show that the currently dominant cropping systems in industrialized countries are not sustainable. We therefore need to develop systems that alleviate this triple 'weed trade-off': i) the use of 'curative' (chemical or mechanical) weed controls must be reduced to limit their negative environmental impacts; ii) the continuous selection for and growth of noxious weed populations must be prevented to allow stable crop yields; while iii) wild plant species and the associated animals must be conserved for the sake of their ecosystem functions and their positive effects for farming systems and for humankind more generally including various ecosystem services. These three aims are often considered contradictory and incompatible, forming different tradeoffs.

Hypothesis: Increasing temporal and spatial crop diversity in crop rotations and landscapes may both be useful components to approach these three aims. Rotating crops that favour different kinds of weed species might be of special interest for weed management and plant diversity, as arable weeds (compared to other crop pests) mostly show rather low spatial but high temporal dispersal abilities (survival in the soil seed bank). Short and simple crop rotations may, for example, be diversified by introducing perennial forage crops (also called 'temporary grasslands'). However, the impacts of such crops on arable weeds are not well understood. The present work aims at reducing this gap in our

Résumé substantiel en Français

Diversification des rotations de grandes cultures avec des prairies temporaires : un moyen pour combiner la gestion de la flore adventice et la conservation de la biodiversité

En dépit d'une soixantaine d'années d'intensification agricole et d'une utilisation massive d'herbicides dans les pays industrialisés, les adventices ('mauvaises herbes') constituent toujours un sérieux problème pour la production agricole. En même temps, la perte dramatique de biodiversité dans les paysages agricoles, la pollution de environnement, les coûts élevés des herbicides et la sélection de plantes résistantes aux herbicides montrent que les systèmes de culture actuellement dominant dans les pays industrialisés ne peuvent être durables. Il est donc urgent de développer des systèmes capables d'amortir le 'triple conflit lié aux adventices' : i) le recours au contrôle 'curatif' des mauvaises herbes (chimique et mécanique) doit être réduit en raison de ses impacts négatifs sur l'environnement; ii) la sélection continue et la croissance démographique des populations adventices doivent être maitrisés pour éviter les pertes de rendement; mais iii) des espèces de plantes sauvages et les animaux associés doivent être conservés et favorisés en raison de leurs fonctions dans l'écosystème et de leur utilité pour l'agro-système et pour l'homme (services écosystémiques). Ces trois objectifs sont souvent considérés comme contradictoires et incompatibles.

Hypothèse : *La diversification temporelle et spatiale des cultures dans les rotations et les paysages pourrait être un moyen de concilier ces trois objectifs. En particulier, la rotation de cultures favorisant chacune différents types d'espèces d'adventices pourrait avoir un intérêt à la fois pour la gestion des adventices et pour la diversité floristique, car les adventices ont des capacités de dispersion spatiale relativement faibles (par rapport à d'autres ravageurs de cultures), mais de fortes capacités de dispersion temporelle (survie dans la banque de graines dans le sol). Des rotations de cultures courtes et simples pourraient être diversifiées par l'introduction de cultures (fourragères) pérennes ('prairies temporaires'). Mais les impacts de ce type de culture sur les adventices des grandes cultures*

Ausführliche Zusammenfassung Deutsch

Diversifizieren von Ackerfruchtfolgen mit temporären Grünländern: Möglichkeiten, Unkrautkontrolle und Biodiversitätsschutz zu kombinieren

Trotz über 60-jähriger Intensivierung der Landwirtschaft inklusive massivem Einsatz von Herbiziden in den Industrieländern stellen Ackerunkräuter (oder ‚Kultur-Begleitkräuter') weiterhin ein großes Problem in der Pflanzenproduktion dar. Gleichzeitig zeigen der dramatische Verlust biologischer Vielfalt in Agrarlandschaften, die Umweltbelastung mit Herbiziden, die hohen Kosten der Pflanzenschutzmittel und die vermehrte Auslese von herbizidresistenten Unkräutern, dass die in den Industrieländern derzeit dominierenden Anbausysteme nicht nachhaltig sind. Wir müssen daher dringend Systeme entwickeln, die das dreifache 'Unkraut-Problem' abschwächen: i) Der Einsatz 'kurativer' (chemischer und mechanischer) Unkrautkontrolle muss wegen deren negativer Auswirkungen auf die Umwelt reduziert werden; ii) die kontinuierliche Selektion und das Wachstum von schädlichen Unkrautpopulationen muss vermieden werden, um dauerhaft stabile Erträge erwirtschaften zu können; iii) wilde Pflanzenarten und die von ihnen abhängigen Tiere müssen erhalten werden, um ihre verschiedenen Funktionen im Ökosystem und positiven Effekten für die Landwirtschaft und die Allgemeinheit (Ökosystem-Dienstleistungen) zu ermöglichen. Diese drei Ziele werden allerdings oft als gegensätzlich und inkompatibel angesehen.

Hypothese: Eine zeitliche und räumliche Diversifizierung der Kulturen innerhalb der Fruchtfolgen und Landschaften könnten dazu beitragen, diese drei Ziele zu erreichen. Besonders der zeitliche Wechsel zwischen verschiedenen Kulturen, die jeweils verschiedene Unkrautarten fördern, könnte sowohl der Unkrautregulierung als auch der Erhaltung der Artenvielfalt dienen, da Ackerunkräuter (im Gegensatz zu anderen Kultur-Schädlingen) geringe räumliche, aber ausgeprägte zeitliche Ausbreitungsmöglichkeiten besitzen (Überleben in der Bodensamenbank). Enge Fruchtfolgen mit wenigen und ähnlichen Kulturen können z.B. durch die Einführung von mehrjährigen (Futter-) Kulturen ('temporäre Grünländer') diversifiziert werden. Die Auswirkungen solcher Kulturen auf Ackerunkräuter sind allerdings kaum bekannt.

Extended summary in English

knowledge. Therefore, the impacts of perennial forage crops on (**1**) weed communities, (**2**) weed population dynamics, (**3**) individual weed plants and (**4**) seed predation of common weed species were studied here.

1) Large-scale weed surveys on 632 fields in western France realized in a 3-year collaborative research project 'ECOGER' showed that differences in weed species composition between perennial forage crops based on alfalfa (*Medicago sativa*) and six annual crops (winter wheat, rape, pea, sunflower, maize, and sorghum) were stronger than the well-known differences between autumn- and spring-sown annual crops. Comparisons of wheat fields following either perennial alfalfa or annual crops suggested that the differences in emerged weed communities may also have long-term effects. A space-for-time substitution design comparing the weed species composition and diversity before, during and after perennial crops (420 fields in total) suggested that weed communities vary in a cyclic way during these phases of long crop rotations. Analysis of indicator species and species functional groups suggested that perennial crops shifted the communities away from annual broad-leaved weed species with an upright or climbing morphology containing several species that are often problematic in annual crops such as cleavers (*Galium aparine*). On the other hand, biennial and perennial species, and annual species with rosettes, benefited from the particular growth conditions in alfalfa. This led to slightly increased species diversities.

2) The mechanisms of these impacts were investigated more closely in a 3-year field experiment. Population dynamics of major arable weed species were compared for perennial forage crops and a succession of annual cereal crops, each with several management options. Overall weed plant densities, aboveground biomasses, and species numbers showed decreasing tendencies in all perennial crop treatments but sometimes strongly increasing tendencies in the annual crops. Among the management options for the perennial crops, the sowing season (autumn vs. spring) often had higher impacts on response variables than crop species

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*ne sont pas bien connus. Le but des travaux présentés ici est de pallier ce manque de connaissances. Pour cela, les effets des cultures fourragères pluriannuelles sur (**1**) la composition des communautés d'adventices, (**2**) les dynamiques de populations, (**3**) des plantes individuelles et (**4**) la prédation de graines d'adventices communes sont étudiées ici.*

***1)** Des relevés floristiques dans 632 champs dans l'ouest de la France réalisés dans le cadre d'un projet de recherche de 3 ans 'ECOGER', montrent que les différences de composition spécifique des communautés adventices, entre des cultures fourragères pérennes à base de luzerne (*Medicago sativa*) et six cultures annuelles (blé d'hiver, colza, pois, tournesol, maïs, et sorgho) sont plus importantes que les différences, mieux connues, entre les cultures d'automne et celles de printemps. La comparaison de champs de blés succédant soit à des luzernes pérennes, soit à des cultures annuelles, suggère que ces différences des communautés peuvent avoir des effets à long terme. Une comparaison de 420 champs avant, pendant, et après des cultures pérennes (basée sur une 'substitution statistique du temps par l'espace') suggère que la composition des communautés varie, selon une trajectoire cyclique pendant ce type de rotation. L'analyse des espèces indicatrices et des groupes fonctionnels d'espèces suggère que les cultures pérennes modifient la composition de la communauté en défavorisant particulièrement les espèces annuelles dicotylédones pourvues d'une morphologie dressée ou grimpante, y compris plusieurs espèces fréquemment problématiques dans des cultures annuelles comme le gaillet* (Galium aparine)*. En revanche, des espèces bisannuelles et pérennes, ainsi que des espèces annuelles pourvues de rosettes, ont été favorisées, ce qui a contribué à augmenter légèrement la diversité spécifique.*

***2)** Les mécanismes impliqués dans ces changements ont été étudiés au cours d'une expérimentation de 3 ans. Les dynamiques de population de plusieurs espèces adventices majeures ont été comparées pour une succession de cultures annuelles et des cultures fourragères pérennes avec différents modes de gestion. De manière générale, les densités de plantes adventices, leurs biomasses et le nombre d'espèces ont montré des tendances à la baisse dans les cultures pérennes mais des hausses parfois très fortes dans les cultures annuelles. Parmi les facteurs de gestion des cultures pérennes, la saison de semis de la culture (automne* vs. *printemps) a souvent eu des impacts plus forts que l'espèce cultivée (luzerne* vs. *dactyle) ou la fréquence*

Ausführliche Zusammenfassung Deutsch

Diese Wissenslücke soll durch die vorliegende Arbeit verkleinert werden. Dazu wurden die Einflüsse mehrjähriger Futterkulturen auf (**1**) die Zusammensetzung der Pflanzengemeinschaften, (**2**) die Populationsdynamiken einzelner Arten, (**3**) die Biomasse individueller Pflanzen, und (**4**) die Samenprädation häufiger Unkrautarten untersucht.

1) Die im Rahmen eines dreijährigen gemeinschaftlichen Forschungsprojekts 'ECOGER' realisierten Vegetationsaufnahmen auf 632 Feldern in Westfrankreich zeigten, dass die Art-Zusammensetzung der Vegetationsgemeinschaften zwischen ausdauernden Futterkulturen basierend auf Luzerne (*Medicago sativa*) und sechs einjährigen Kulturen (Winterweizen, Raps, Erbsen, Sonnenblumen, Mais und Sorghum) stärker variierten als der gut bekannte Unterschied zwischen im Herbst und im Frühling gesäten einjährigen Kulturen. Der Vergleich von Weizenfeldern, die entweder auf mehrjährige Luzerne oder auf verschiedene einjährige Kulturen folgten, zeigte, dass die oben beschriebenen Unterschiede der Begleitvegetation auch Langzeiteffekte haben können. Ein Vergleich von 420 Feldern vor, während, und nach mehrjährigen Futterkulturen (basierend auf einem statistischen ‚Raum-Zeit-Ersatz') lässt vermuten, dass die Zusammensetzung der Unkrautgemeinschaften im Laufe solcher Fruchtfolgen zirkulär variiert. Eine Analyse der Indikator-Arten und funktioneller Gruppen zeigte, dass die ausdauernden Futterkulturen besonders die aufrechten und kletternden Unkräuter der einjährigen zweikeimblättrigen Arten zurückdrängten. Unter diesen Arten befanden sich viele, die in einjährigen Kulturen oft problematisch sind, wie z.B. das Klebkraut (*Galium aparine*). Auf der anderen Seite konnten zwei- und mehrjährige Arten, sowie einjährige Arten mit Rosetten, profitieren. Dadurch wurde die Artenvielfalt insgesamt leicht erhöht.

2) Die diesen Veränderungen zugrunde liegenden Mechanismen wurden in einem drei Jahre dauernden Feldversuch näher untersucht. Dabei wurden die Populationsdynamiken häufiger Ackerunkräuter in einjährigen und ausdauernden Kulturen mit jeweils unterschiedlichen Bearbeitungsoptionen verglichen. Die Dichte der Unkrautpflanzen, die oberirdische Biomasse und die Anzahl der Arten zeigten abnehmende Tendenzen in allen Bearbeitungsoptionen der mehrjährigen Kulturen, und teils stark ansteigende Tendenzen in den einjährigen Kulturen. Der Vergleich der Bearbeitungsoptionen zeigte, dass der Aussaatzeitpunkt der mehrjährigen Kulturen (Herbst/Frühling) meist einen größeren Einfluss hatte als die Kulturart (Luzerne /Knaulgrass) oder

(alfalfa vs. cocksfoot) and cutting frequency (3 vs. 5 cuts per year). The behaviour of individual species and functional groups corresponded mostly to those observed in the large-scale weed surveys (part 1).

de fauche (3 vs. 5 fois par an). Le comportement des espèces individuelles et des groupes fonctionnels s'est montré globalement cohérent avec les résultats des relevés à large échelle (partie 1).

die Schnitthäufigkeit (3/5 Schnitte pro Jahr). Die Reaktion einzelner Arten und funktioneller Gruppen entsprach meist dem in den großflächigen Vegetationsaufnahmen (Teil 1) beobachteten Verhalten.

The results of these two studies suggest that several stages of the weed life cycle were affected by three characteristics of perennial forage crops. (A) The complete absence of soil tillage reduced weed emergence, increased survival of established weed plants, and probably reduced weed seed survival, e.g. due to increased seed predation. (B) Temporally extended competition by perennial crops and (C) hay cuttings reduced the vegetative weed growth and weed seed production. Some of these mechanisms, including the impacts of soil tillage and competition on weeds, are quite well known in the literature, in contrast to the impacts of cuttings and weed seed predation. Therefore, specific experiments were conducted here to better understand these two mechanisms (parts 3 and 4).

Les résultats de ces deux études suggèrent que trois caractéristiques des cultures fourragères pérennes affectent plusieurs stades du cycle de vie des adventices : (A) l'absence complète de travail du sol réduit la levée des adventices, augmente la survie des plantes adventices établies et réduit probablement la survie des graines, par exemple par une augmentation de la prédation de graines ; (B) la compétition qui s'exerce sur un temps plus longue, et (C) les fauches contribuent à réduire la croissance végétative et la production de graines des adventices. Quelques-uns de ces mécanismes, comme le travail du sol et la compétition avec la culture, sont déjà relativement bien connus dans la littérature, ce qui n'est pas le cas pour les impacts de la fauche et de la prédation des graines. Pour cette raison, des expérimentations spécifiques ont été menées ici pour mieux comprendre ces deux mécanismes (parties 3 et 4).

Die Ergebnisse dieser beiden Studien legen nahe, dass drei Charakteristika der mehrjährigen Kulturen mehrere Lebensstadien der Ackerunkräuter beeinflussten: (A) Das Fehlen jeglicher Bodenbearbeitung reduzierte das Auflaufen von Unkräutern, erhöhte das Überleben von etablierten Unkrautpflanzen und verminderte vermutlich das Überleben von Unkrautsamen, z.B. durch verstärkte Samenprädation. (B) Die zeitlich ausgedehnte Konkurrenz der mehrjährigen Kulturen sowie (C) die häufigen Heuschnitte reduzierten das vegetative Unkrautwachstum und die Unkrautsamenproduktion. Einige dieser Mechanismen, etwa die Einflüsse von mechanischer Bodenbearbeitung und Konkurrenz mit der Kultur, sind in der Literatur schon relativ gut bekannt, im Gegensatz zu den möglichen Einflüssen von Heuschnitten und Samenprädation. Letztere Mechanismen wurden daher durch spezifische Experimente (Teile 3 und 4) näher untersucht.

3) The impacts of cutting and the regrowth abilities of weeds and crops were analyzed first on individual plants in the greenhouse. Removing large parts of aboveground plant organs by manual cutting had negative effects on total (cumulative) biomass production of all tested species (weeds and crops), but the regrowth abilities of annual broadleaved weeds were much lower than for annual grass weeds and perennial forage crops, matching the observations from the large scale surveys and the field experiment. Differences between weed species may partly be explained by their specific morphology and life cycle (phenology). The morphology may determine both the quantity of leaf area remaining after the cuttings (needed for photosynthesis) and the quantity of meristems / buds (needed for regrowth). The phenology may determine the morphology at the moment of cutting and the quantity of belowground resources that may be remobilized for regrowth.

3) *Les impacts des fauches et les possibilités de croissance post-fauche des plantes adventices et cultivées ont d'abord été analysés sur des plantes individuelles en serre. La destruction d'une grand partie des organes aériens des plantes par des fauches manuelles a eu des effets négatifs sur la production totale (cumulée) de biomasse de toutes les espèces testées (adventices et cultures), mais les capacités de croissance post-fauche des espèces dicotylédones annuelles étaient beaucoup moins fortes que celles des graminées annuelles et des espèces fourragères pérennes, ce qui est en accord avec les résultats de l'expérimentation au champ et des relevés à grande échelle. Les différences entre les espèces peuvent en partie être expliquées par leur morphologie et par leur cycle de vie (phénologie). La morphologie peut à la fois déterminer la surface foliaire subsistant après la fauche (pour la photosynthèse) et le nombre de bourgeons (permettant de continuer la croissance). La phénologie des espèces peut déterminer la morphologie au moment de la coupe et la quantité de ressources souterraines remobilisables pour la croissance post-fauche.*

3) Die Fähigkeit von Unkraut- und Kulturpflanzen, nach Schnittmaßnahmen weiterzuwachsen, wurde zuerst an einzelnen Pflanzen im Gewächshaus untersucht. Die Zerstörung eines großen Teils der oberirdischen Pflanzenorgane durch manuelle Schnitte hatte negative Auswirkungen auf die gesamte (kumulierte) Biomasseproduktion bei allen getesteten Arten (Unkräuter und Kulturen). Die Fähigkeit, nach Schnittmaßnahmen weiterzuwachsen, war allerdings bei aufrechten einjährigen zweikeimblättrigen Arten viel geringer als bei Gräsern sowie mehrjährigen Kulturarten, was den vorherigen Beobachtungen auf den kommerziellen Feldern und dem Feldversuch entspricht. Diese Unterschiede können teilweise mit der Wuchsform der Arten so wie deren Lebenszyklus (Phänologie) erklärt werden. Die Wuchsform kann sowohl die Größe der Blattfläche (für die Photosynthese), als auch die Menge der (für das Nachwachsen benötigten) Knospen, die nach dem Schnitt noch vorhanden sind, beeinflussen. Die Phänologie der Arten bestimmt unter anderem deren Morphologie zum Schnittzeitpunkt und kann die Menge der unterirdische Ressourcen beeinflussen, die für das Nachwachsen mobilisiert werden können.

For plants of the same species and same age, regrowth speed was positively correlated with plant biomass before cutting. This suggests that bigger plants can remobilize more belowground carbohydrate resources for regrowth.

Pour des plantes de la même espèce et du même âge, la vitesse de croissance post-fauche est positivement corrélée avec la biomasse avant coupe. Cela indique que l'état de croissance au moment de la fauche affecte la disponibilité des ressources remobilisables

Bei Pflanzen gleicher Art und gleichen Alters war die Geschwindigkeit des Nachwachsens positiv mit der Biomasse der Pflanzen vor dem Schnitt korreliert. Dies deutet darauf hin, dass größere Pflanzen mehr mobilisierbare Ressourcen haben. Außerdem nahm die Geschwindigkeit des

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When comparing weed plants of different ages, the regrowth capacity was reduced for older plants, where resources are probably already remobilized for reproduction. In field conditions, the regrowth capacity of weeds may also depend on the competitive environment before and after cutting, thus also on the regrowth speed of neighbouring (forage crop) plants. A study on experimental plant communities in the greenhouse with a 2x2 factorial design suggested that the negative effects of cutting and competition on weed biomass production are mainly additive. The combination of both treatments thus resulted in the lowest weed biomass production.

4) Weed seed predation might be more important in perennial crops compared to annual crops, as newly produced seeds stay longer on the soil surface, accessible to seed eating animals. A series of field experiments on seven weed species showed that the seeds of some species are much more eaten than others. Seed predation may thus be another reason for the changes in weed community composition observed after perennial crops.

Moreover, perennial crops might constitute a favourable habitat for weed seed predators due to the absence of soil tillage and the permanent vegetation cover. This was tested in another field experiment, which suggested that seed predation by both vertebrates (over 12mm in diameter) and invertebrates (under 12 mm) increased with vegetation cover. Mowing treatments (cut vs. uncut) had a much stronger (negative) influence on predation rates than the forage crop species (alfalfa vs. cocksfoot). The quantity of aboveground vegetation was thus more important than its quality.

Conclusion: These various results agree with the initial hypothesis that perennial forage crops create conditions that are unfavourable to many typical weed species including those that are problematic in annual crops. On the other hand, other less problematic plant species may profit from the specific conditions. Integrating perennial forage crops into crop rotations may thus be used as a part of Integrated Weed Management and may reduce the need for herbicide applications. At the same

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pour la croissance post-fauche. La comparaison de plantes d'âges différents a montré que la capacité de croissance post-fauche diminue avec l'âge (malgré une plus grande taille), probablement en raison de la remobilisation de ressources pour la croissance des organes reproducteurs. Au champ, la capacité de croissance post-fauche peut également dépendre de l'environnement compétitif avant et après la fauche, et donc aussi de la vitesse de croissance post-fauche des plantes voisines (de la culture fourragère et d'autres adventices). Une étude sur des communautés expérimentales de plantes avec deux facteurs croisés a suggéré que les effets négatifs de la fauche et de la compétition sur la production de biomasse des adventices sont souvent additifs, la production de biomasse était donc la moins importante lorsque les deux traitements étaient combinés.

***4)** La prédation de graines d'adventices peut être plus importante dans des cultures pérennes que dans des cultures annuelles, car les graines nouvellement produites restent plus longtemps en surface du sol, accessibles pour des animaux granivores. Une série d'expérimentations au champ avec sept espèces adventices a montré que les graines de certaines espèces sont souvent préférées à d'autres. La prédation de graines peut donc être une autre cause des changements de la composition des communautés observés après les cultures pérennes.*

De plus, les cultures pérennes pourraient constituer un habitat favorable pour des prédateurs de graines en raison de l'absence de travail du sol et de la couverture permanente par la végétation. Cette hypothèse à été testée avec une expérimentation au champ suggérant que la prédation de graines par des vertébrés (diamètre >12mm) et par des invertébrés (<12mm) augmente avec le couvert végétal. Des traitements de fauche (fauché vs. *non fauché) ont eu un impact (négatif) beaucoup plus fort que la nature de l'espèce cultivée (luzerne* vs. *dactyle). La quantité de végétation aérienne est donc plus importante que sa qualité.*

***Conclusion :** Ces résultats sont en accord avec l'hypothèse initiale que les cultures fourragères pérennes créent des conditions défavorables pour des espèces adventices problématiques dans les grandes cultures annuelles. En contrepartie, d'autres espèces végétales moins problématiques en culture annuelle peuvent profiter des conditions spécifiques. L'intégration de prairies temporaires dans des rotations de cultures annuelles peut donc être utilisée comme une composante de la gestion intégrée des adventices, permettant ainsi de réduire le*

Ausführliche Zusammenfassung Deutsch

Nachwachsens mit dem Alter der Pflanzen ab (trotz höherer Biomasse), was daran liegen könnte, dass die Ressourcen teilweise schon für generatives Wachstum verwendet wurden. Die Nachwuchs-Fähigkeit von Unkräutern hängt auch von den allgemeinen Wachstumsbedingungen ab, die wiederum unter anderem von der Konkurrenzsituation vor und nach der Schnittmaßnahme abhängen, also auch von der Nachwachsgeschwindigkeit der benachbarten Kultur- und Unkrautpflanzen. Eine Untersuchung an experimentellen Pflanzengemeinschaften mit zwei gekreuzten Faktoren legte nahe, dass die negativen Effekte der Schnittmaßnahmen und der Konkurrenz auf die Unkrautbiomasseproduktion meistens additiv sind, d.h. die Kombination beider Behandlungen führte zu der geringsten Biomasseproduktion der Unkräuter.

4) Die Prädation von Unkrautsamen könnte in ausdauernden Kulturen ausgeprägter sein als in einjährigen, da die neu gebildeten Samen länger auf der Bodenoberfläche bleiben, wo sie Samen fressenden Tieren am besten zugänglich sind. Eine Serie von Feldversuchen mit sieben Unkrautarten zeigte, dass die Samen mancher Arten viel häufiger gefressen werden als die anderer Arten. Samenprädation kann daher eine weitere Ursache für die beobachteten Änderungen der Pflanzengesellschaften nach mehrjährigen Kulturen sein.

Außerdem könnten mehrjährige Kulturen durch die fehlende Bodenbearbeitung und die permanente Vegetation ein günstiges Habitat für Samenprädatoren darstellen. In einem Feldexperiment wurde der Einfluss der Vegetationsbedeckung auf die Samenprädation getestet und positive Zusammenhänge sowohl für Wirbeltiere (über 12mm Durchmesser) als auch für Wirbellose (unter 12mm) festgestellt. Der Grassschnitt (geschnitten/ungeschnitten) hatte einen viel größeren (negativen) Einfluss auf die Prädationsraten als die Kulturart (Luzerne/Knaulgrass). Die Menge an oberirdischer Vegetation war daher wichtiger als deren Qualität.

Schlussfolgerung: Diese verschiedenen Ergebnisse stimmen mit der anfänglichen Hypothese überein, dass ausdauernde Futterkulturen Bedingungen erzeugen, an die viele typische Ackerunkräuter – inklusive der in einjährigen Kulturen sehr problematischen Arten – nicht angepasst sind. Dahingegen können andere, weniger problematische Arten von den stark veränderten Bedingungen profitieren. Das Hereinnehmen mehrjähriger Futterkulturen in die Fruchtfolge kann daher als Teil eines ‚Integrierten Unkrautmanagements' genutzt werden, und dazu beitragen, Herbizide

time, increasing the temporal and spatial crop and landscape diversity with perennial crops (combined with agri-environment schemes such as overwinter stubble fields) may increase plant diversity and the provision of food resources for endangered farmland wildlife. The diversification of crop rotations with perennial crops thus has the potential to circumvent the 'weed trade-offs'. These advantages for weed management and biodiversity add to the other, better known functions of perennial crops including the reduction of soil erosion and nitrogen leaching, increases in soil organic matter and the biological nitrogen fixation of legume crops.

Perspectives: Future studies must analyze the economic feasibility of such farming systems and whether other perennial crops such as new biomass or energy crops may be used instead of forage crops to reduce the 'weeds trade-off'. The factors and mechanisms determining the impacts of perennial crops on weeds described in this thesis might be used to supplement simulation models (such as FLORSYS). Such models may be used to study and predict weed population dynamics in cropping systems including both annual and perennial crops.

Key words English[1]

Agroecology, Integrated Weed Management, crop rotation, temporary grassland, perennial forage crops, *Medicago sativa*, plant community composition, functional group, population dynamics, post-cutting regrowth dynamics, seed predation, granivory, biological pest control, ecosystem service.

besoin d'utilisation d'herbicides. En même temps, la diversification temporelle et spatiale du paysage avec des cultures pérennes (combinées éventuellement avec d'autres mesures agri-environnementales comme le maintien de chaumes en hiver) pourrait augmenter la diversité floristique et la mise à disposition de ressources trophiques pour des espèces animales en danger dans les paysages agricoles. La diversification des rotations peut donc contribuer à résoudre les trois problèmes liés aux adventices. Ces effets positifs pour la gestion des adventices et pour le maintien de la biodiversité s'ajoutent aux autres avantages des cultures pérennes comme l'augmentation de la matière organique, la réduction de l'érosion du sol et du lessivage de nutriments, et la fixation biologique de l'azote chez les légumineuses.

***Perspectives**: Des études futures devraient analyser la performance économique de ces systèmes de culture. On devrait aussi tester si l'intégration d'autres cultures pérennes comme des nouvelles cultures productrices de biomasse ou d'énergie pourraient être intégrées dans les pour amortir les problèmes liés aux adventices. Les facteurs et mécanismes déterminant les impacts des cultures pérennes sur les adventices analysés dans cette thèse pourraient être utilisés pour compléter des modèles de simulation d'adventices (tels que FLORSYS). De tels modèles pourront être utilisés pour étudier et prédire les dynamiques de populations d'adventices dans des systèmes incluant des cultures annuelles et pérennes.*

Mots clés Français

Agro-écologie, protection intégrée, rotation des cultures, prairie temporaire, culture pérenne fourragère, Medicago sativa, *composition de communauté de plantes, groupe fonctionnel, dynamique de population, croissance post-fauche, prédation de graines, granivorie, lutte biologique, service écosystémique.*

einzusparen. Gleichzeitig können mehrjährige Kulturen (evtl. in Kombination mit anderen in die Fruchtfolge integrierten Agrar-Umweltmaßnahmen wie Stoppelbrachen im Winter) die räumliche und zeitliche Landschaftsvielfalt und Pflanzendiversität erhöhen und das Nahrungsangebot für wildlebende Tiere verbessern. Die Diversifizierung der Fruchtfolgen mit ausdauernden Kulturen kann also einen Beitrag dazu leisten, das oben beschriebene dreifache ‚Unkrautproblem' abzumildern. Diese unkrautregulierende und biodiversitätsfördernde Funktion kommt zu den anderen, besser bekannten positiven Auswirkungen mehrjähriger Kulturen, wie z.B. die Zunahme an organischer Substanz im Boden, die Verminderung von Bodenerosion und Nährstoffauswaschung, und die biologische Stickstofffixierung bei Leguminosen, noch hinzu.

Ausblick: Bei zukünftigen Studien sollte die ökonomische Machbarkeit solcher Anbausysteme untersucht werden. Ebenso könnte getestet werden, ob die Integration anderer ausdauernder Kulturen (wie die neuen Biomasse- und Energiekulturen) in die Fruchtfolgen integriert werden können, um die ‚Unkraut-Probleme' zu reduzieren. Die in dieser Arbeit dargestellten Faktoren und Mechanismen der Einflüsse von mehrjährigen Futterkulturen auf Ackerunkräuter können auch dazu verwendet werden, Unkraut-Simulationsmodelle (wie FLORSYS) zu vervollständigen. Solche Modelle können dazu dienen, die Dynamiken von Unkrautpopulationen in Anbausystemen mit ein- und mehrjährigen Kulturen zu studieren und vorhersagen zu können.

Deutsche Stichwörter

Agrarökologie, Integrierter Pflanzenschutz, Fruchtfolge, Temporäres Grünland, Mehrjährige Futterkultur, *Medicago sativa*, Zusammensetzung der Pflanzengemeinschaft, Funktionelle Gruppe, Populationsdynamik, Nachwachsen nach Schnittmaßnahmen, Samenprädation, Biologische Schädlingsbekämpfung, Ökosystemdienstleistung.

[1] More key words and technical terms in English, French and German are found in Annexe 1.

SHORT VERSIONS (ABOUT 270 WORDS)

Short summary in English

Crop rotation may be used to prevent the continuous selection of particular weed species adapted to one crop type. This might be useful for weed management, economy in herbicide applications and promoting biodiversity. Common simple crop sequences might be diversified by introducing perennial forage crops. Impacts of such perennial crops on weeds were studied with four approaches:

1) Large-scale weed surveys in 632 fields in western France showed that weed species composition differed most strongly between perennial alfalfa crops and annual crops. Comparisons of fields before, during and after perennial alfalfa suggested that community composition varies in a cyclic way during such crop rotations. Several weed species problematic in annual crops were suppressed during and after perennial crops, but the appearance of other species led to equal or even higher plant diversities.

2) A 3-year field experiment with contrasting crop management options allowed an investigation of the underlying mechanisms for this: The absence of soil tillage reduced weed emergence but increased the survival of established plants. The permanent vegetation cover and frequent hay cuttings reduced weed growth, plant survival and seed production.

3) Greenhouse experiments testing the regrowth ability of individual plants after cutting showed strong differences between species and functional groups. An two-factorial experiment suggested that the negative impacts of cutting and competition on weed growth were mainly additive.

4) Special measurements of weed seed predation in the field experiment showed positive correlations with vegetation cover, indicating that this ecosystem service may be particularly fostered by perennial crops. Consistent preferences of seed predators for certain weed species indicates that seed predation may be another cause of the observed weed community shifts.

More details may be found in the extended summaries (in English, French, and German), page XI.

Résumé court en français

La rotation de cultures peut être utilisée pour empêcher la sélection continue d'espèces adventices adaptées à un type de culture. Elle pourrait favoriser la gestion des adventices, l'économie d'herbicides et la biodiversité. Les successions de cultures simples d'aujourd'hui pourraient être diversifiées par des cultures fourragères pérennes. Les impacts des ces cultures sur les adventices ont été étudié utilisant quatre approches :

1) *Des relevés d'adventices sur 632 champs dans l'ouest de la France ont montré que la composition spécifique varie le plus entre des cultures fourragères pérennes et des cultures annuelles. Une comparaison des champs avant, pendant, et après des cultures fourragères pérennes a suggéré que la composition des communautés varie d'une manière cyclique pendant ces rotations. Plusieurs espèces problématiques dans des cultures annuelles ont été supprimées pendant et après les cultures pérennes, mais l'apparition d'autres espèces a produit une diversité de plantes comparable, voire supérieure.*

2) *Une expérimentation au champ de trois ans avec des modes de gestion contrastés a permis d'étudier les mécanismes sous-jacents: L'absence de travail du sol a réduit la levée des adventices, mais a augmenté la survie des plantes adultes. Le couvert végétal permanent et les fauches fréquentes ont réduit la croissance, la survie des plantes et la production de graines.*

3) *Des expérimentations sous serre analysant la croissance poste fauche de plantes individuelles ont montré des différences importantes entre espèces et groupes fonctionnels. Une expérimentation à deux facteurs a suggéré que les impacts négatifs de la fauche et de la compétition sur la croissance des adventices ont été additifs.*

4) *Des mesures spéciales de prédation de graines d'adventices sur l'expérimentation au champ ont montré des corrélations positives avec le couvert végétal et la prédation, indiquant une importance particulière de ce service écosystémique dans des cultures pérennes. La préférence des graines de certaines espèces montre que la prédation de graines peut être une autre cause des changements de communautés d'adventices.*

Pour plus de détails, voir les résumés substantiels (en français, anglais et allemand), page XI.

Kurze Zusammenfassung auf Deutsch

Fruchtfolgen können dazu dienen, die kontinuierliche Selektion von Unkrautarten zu verhindern, die an eine bestimmte Kultur angepasst sind. Dies könnte dem Unkrautmanagement, der Einsparung von Herbiziden, und der Biodiversität dienen. Heutige, sehr einfache Furchtfolgen könnten durch mehrjährige Futterkulturen diversifiziert werden. Die Einflüsse solcher mehrjähriger Kulturen auf Unkräuter wurden in vier Ansätzen untersucht:

1) Vegetationsaufnahmen auf 632 Feldern in Westfrankreich zeigten, dass die Unkrautzusammensetzung zwischen mehrjährigen Futterkulturen und einjährigen Kulturen stark variiert. Der Vergleich von Feldern vor, während und nach mehrjährigen Futterkulturen legte nahe, dass die Pflanzengemeinschaft während solcher Fruchtfolgen zyklisch variiert. Mehrere problematische Unkrautarten wurden während und nach den mehrjährigen Kulturen zurückgedrängt. Das Auftauchen anderer Arten führte jedoch zu einer gleichbleibenden oder leicht erhöhten Pflanzenvielfalt.

2) Ein dreijähriger Feldversuch mit verschiedenen Bearbeitungsoptionen ermöglichte es, die zugrunde liegenden Mechanismen zu untersuchen: Die fehlende Bodenbearbeitung hat das Auflaufen der Unkräuter reduziert und das Überleben der adulten Pflanzen erhöht. Die permanente Vegetationsbedeckung und die häufigen Heuschnitte haben das Wachstum, das Überleben und die Samenproduktion vermindert.

3) Gewächshausexperimente zum Nachwachsen von Unkrautpflanzen nach Heuschnitten zeigten große Unterschiede zwischen verschiedenen Arten und funktionellen Gruppen. Ein Experiment mit zwei Faktoren lässt vermuten, dass die negativen Effekte der Schnitte und der Konkurrenz auf das Unkrautwachstum sich addieren.

4) Spezielle Messungen der Prädation von Unkrautsamen auf den untersuchten Feldern zeigten positive Korrelationen mit der Vegetationsbedeckung, was auf eine besondere Wichtigkeit dieser Ökosystemdienstleistung in ausdauernden Kulturen hindeutet. Die Präferenz von bestimmten Samenarten deutet darauf hin, dass Samenprädation ein weiterer Grund für die beobachteten Änderungen der Unkrautgemeinschaften sein kann.

Mehr Details können den ausführlichen Zusammenfassungen (auf Deutsch, Englisch und Französisch) auf Seite XI entnommen werden.

CONTEXT AND FUNDING

This thesis is the result of a bi-national PhD project (‘*cotutelle internationale de thèse*’ /’joint supervision of doctorates’ /‘*Binationales Promotionsverfahren*’) between the *Université de Bourgogne* in Dijon, France and the *Justus-Liebig-Universität Gießen* in Germany.

In France, the thesis was supervised by Dr. Jacques CANEILL, professor, and co-supervised by Dr. Nicolas MUNIER-JOLAIN, *ingénieur de recherche*, who both belong to the research group ‘UMR 1210 *Biologie et Gestion des Adventices*’ (BGA, weed biology and management) in Dijon[2]. This laboratory jointly belongs to the *Institut National de la Recherche Agronomique* (INRA[3]), the *Institut national supérieur des sciences agronomiques de l’alimentation et de l’environnement* (AgroSup Dijon[4]), and the *Université de Bourgogne* (uB[5]) and is headed by Dr. Xavier REBOUD, *directeur de recherche*.

In Germany, the thesis was supervised by Dr. Rainer WALDHARDT, professor, who belongs to the ‘Division of Landscape Ecology and Landscape Planning[6]‘ headed by Dr. Dr. Annette OTTE, professor, which is part of the ‘Institute of Landscape Ecology and Resources Management[7]‘ and the ‘Research Centre for Bio Systems, Land Use and Nutrition’ (IFZ[8]) of the Justus-Liebig-University Giessen. Dr. Bernd HONERMEIER, professor at the ‘Institute of Crop Science and Plant Breeding I’ (IPZ[9]) of the Justus-Liebig-University was the co-supervisor in Germany.

The PhD project is scientifically embedded in:

- the ECOGER project (*ÉCOlogie pour la Gestion des Écosystèmes et de leurs Ressources*, financed by INRA and ADEME)[10]. The correspondent sub-project is called ‘*Gestion durable des ressources naturelles en plaine céréalière: le rôle central des surfaces pérennes dans les agro-écosystèmes céréaliers*’, headed by Dr. Vincent BRETAGNOLLE,

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[2] http://www2.dijon.inra.fr/bga/umrbga2009 accessed on 11 March 2010
[3] http://www.inra.fr
[4] http://www.agrosupdijon.fr/
[5] http://www.u-bourgogne.fr
[6] http://www.uni-giessen.de/cms/faculties/f09/institutes/ilr/loek-en/home
[7] http://www.uni-giessen.de/cms/faculties/f09/institutes/ilr
[8] http://www.uni-giessen.de/cms/fbz/zentren/ifz
[9] http://www.uni-giessen.de/~gh1262/ipz/ipz.html, accessed on 11 Mars 2010
[10] http://www.inra.fr/les_partenariats/programme_federateur_ecoger, accessed on 20 Oct. 2009 and http://www.zaplainevaldesevre.fr, accessed on 11 Mars 2010

directeur de recherche at the UPR 1934 '*Centre d'Études Biologiques de Chizé*' (CEBC) of the *Centre national de la recherche scientifique* (CNRS) ;

- the two framework programs of the weed research group UMR '*Biologie et Gestion des Adventices*' in Dijon (2007-2010): 1) '*Traits de vie et systèmes de culture*'[11] and 2) '*Influence de l'organisation spatiale du territoire sur les populations et les communautés d'adventices*'[12], which are part of '*Agroécologie*', a program that involves several research groups at INRA Dijon ; and

- the research program on 'agricultural ecology' of the 'Division of Landscape Ecology and Landscape Planning'[13] at the Justus-Liebig-University Giessen.

The experimental research was mainly effectuated at INRA Dijon (at the experimental farm 'Epoisses' and in the greenhouses), the weed surveys on commercial fields were done in the CNRS-Chizé study region.

The research received funding from the following institutions and projects:

- the ECOGER-Chizé project (see above),

- the French ANR project SYSTERRA-ADVHERB[14],

- the UMR '*Biologie et Gestion des Adventices*' (see above),

- the ENDURE Network 'Diversifying crop protection'[15],

- AgroSup Dijon (Appel d'Offre Interne, AOI de l'ENESAD 2007-2008)[16],

- the Division of Landscape Ecology and Landscape Planning of Giessen University (see above).

The PhD candidate was funded for 3 years (Oct. 2006 - Sept. 2009) by the French Research Ministry[17] (*allocataire de recherche*).

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[11] http://www2.dijon.inra.fr/bga/umrbga2009/spip.php?article21, accessed on 11 Mars 2010.
[12] http://www2.dijon.inra.fr/bga/umrbga2009/spip.php?article22, accessed on 11 Mars 2010.
[13] http://www.uni-giessen.de/cms/faculties/f09/institutes/ilr/loek-en/main-fields-of-activity/view?set_language=en, accessed on 20 Oct. 2009.
[14] http://www2.dijon.inra.fr/bga/umrbga/squelettes/pieces/Advherb.pdf, accessed on 11 Mars 2010.
[15] http://www.endure-network.eu, accessed on 20 Oct. 2009.
[16] http://www.enesad.fr, accessed on 11 Mars 2010.

THESIS ORGANISATION

This thesis entitled 'Diversifying crop rotations with temporary grasslands: potentials for weed management and farmland biodiversity' is composed of four parts (A-D). Part A ('General Introduction') exposes the problem, introduces possible solutions arising from a literature review, and defines the research questions. These questions are studied using four empirical approaches that are summarized in part B ('Overview of Materials & Methods'). The results are presented in part C, which is divided in four chapters (C.I - C.IV) corresponding to the four empirical approaches. Each of them is constituted of one, two, or three scientific articles or manuscripts (Articles 1-8), where the present author figures as the first author (6) or as a co-author (2). The contribution of the present author to these eight articles and manuscripts is detailed in Table 1. Most of the articles have already been published or accepted for publication, others are 'in preparation'. Published articles are reproduced with kind permission from EDP Sciences (Article 1), John Wiley and Sons (Article 2), Eugen Ulmer (Articles 4 and 6), and Elsevier (Article 8). Of course, each article has its own introduction, methods, results and discussion sections. A General Discussion (part D) summarizes and links the different findings presented in the articles, shows the strength and limits of the methods and discusses some perspectives. The Reference section (part E) contains the literature sources cited in the whole thesis including the articles. The Annexes comprise (i) a translation of about 35 key words and other technical expressions in English, French and German, (ii) a short definition and discussion of the term 'weed', and (iii) a list of all weed species observed in the large-scale surveys, their frequency of occurrence, and information on the species functional groups.

[17] http://www.enseignementsup-recherche.gouv.fr, accessed on 11 Mars 2010.

LIST OF PUBLICATIONS

Articles & manuscripts

Chapter C.I
Impacts of temporary grasslands on weed communities (Chizé)

1) Meiss, H., Médiène, S., Waldhardt, R., Caneill, J. & Munier-Jolain, N. (2010a) Contrasting weed species composition in perennial alfalfa and six annual crops: implications for Integrated Weed Management. *Agron. Sustain. Dev.* **30**, 657-666.

2) Meiss, H., Médiène, S., Waldhardt, R., Caneill, J., Bretagnolle, V., Reboud, X. & Munier-Jolain, N. (2010b) Perennial alfalfa affects weed community trajectories in grain crop rotations. *Weed Research* **50**, 331-340.

Chapter C.II
Experimental analyses of the impacts of temporary grasslands on weed populations

3) Meiss H, R Waldhardt, J Caneill, N Munier-Jolain (in preparation) Mechanisms affecting population dynamics of weeds in perennial forage crops.

Chapter C.III
Regrowth after cutting

4) Meiss, H., Munier-Jolain, N., Henriot, F. & Caneill, J. (2008b) Effects of biomass, age and functional traits on regrowth of arable weeds after cutting. *J. Plant Dis. Prot.*, **XXI**, 493-499.

5) Meiss, H., Bonnot, R., Strbik, F., Waldhardt, R., Caneill, J. & Munier-Jolain, N. (2009) Cutting and competition reduce weed growth: additive or interactive effects? *XIIIth International Conference on Weed Biology*, pp. 28-37. Dijon, France.

Chapter C.IV
Weed seed predation

6) Alignier, A., Meiss, H., Petit, S. & Reboud, X. (2008) Variation of post-dispersal weed seed predation according to weed species, space and time. *J. Plant Dis. Prot.*, **XXI**, 221-226.

7) Cordeau, S.; Meiss, H.; Boursault, A. (2009) Bandes enherbées: Quelle flore, quelles prédateurs, quelle prédation? *XIIIth International Conference on Weed Biology*, 50-59, Dijon, France.

8) Meiss, H., Lagadec, L. L., Munier-Jolain, N., Waldhardt, R. & Petit, S. (2010c) Weed seed predation increases with vegetation cover in arable fields. *Agriculture, Ecosystems & Environment*. **138**, 10-16.

Author's contribution

The contribution of H.M. to the eight articles and manuscripts is detailed in Table 1.

Table 1: Contribution of the author to the research articles and manuscripts.

Chapter of the thesis	**Article or ms** (see list above)	**Idea and design**	**Data collection (field, greenhouse, lab)**	**Data analyses**	**Writing**
C.I Weed surveys Chizé	Article **1**: Current crops (Meiss *et al.*, 2010a, ASD)	1-2	2	1	1
	Article **2**: Trajectories (Meiss *et al.*, 2010b, WRE)	1-2	2	1	1
C.II Field experiments Epoisses	Manuscript **3**: Management options (Meiss *et al.*, in preparation)	1	1-2	1	1
C.III Greenhouse experiments Dijon	Article **4**: Regrowth (Meiss *et al.*, 2008, JPDP)	1	1-2	1	1
	Article **5**: Regrowth & competition (Meiss *et al.*, 2009, ICWB)	1	1-2	1	1
C.IV Seed predation experiments	Article **6**: Weed species (Alignier *et al.*, 2008, JPDP)	2-3	2-3	1-2	1-2
	Article **7**: Field margin strips (Cordeau *et al.*, 2009a, ICWB)	2	2	2	2
	Article **8**: Vegetation cover (Meiss *et al.*, 2010c, AGEE)	1	1-2	1	1

1, H.M. did most of the part and was assisted by his supervisors and the other co-authors*.

2, H.M. contributed substantially in the framework of co-operations with other researchers or students*.

3, This part was mainly done by other participants in the framework of co-operations*.

* The names of co-authors and the contributions of other collaborators are acknowledged in the articles.

Talks

1) Meiss, H., Munier-Jolain, N., Henriot, F. & Caneill, J. (2008) Regrowth of arable weeds after cutting. *24th German Conference on Weed Biology and Weed Control*. Hohenheim, Germany, p. 493-499.

2) Meiss, H., Le Lagadec, L., Petit, S. & Waldhardt, R. (2008) Impacts of vegetation cover and crop identity on weed seed predation. EURECO-GFÖ 'Biodiversity in an Ecosystem Context' – *11th European Ecological Conference of the European Ecological Federation* and *38th Ann. Conf. Ecological Society of Germany, Switzerland and Austria (GfÖ).* Leipzig, Germany, p. 505.

3) Meiss, H.; Le Lagadec, L.; Munier-Jolain, N.; Waldhardt, R. & Petit, S. (2009), Post-dispersal seed predation of 7 weed species increases with vegetation cover, in *3rd Workshop of the EWRS Working Group: Weeds and Biodiversity*, Lleida, Spain, p. 95-96.

4) Meiss, H., Bonnot, R., Strbik, F., Waldhardt, R., Caneill, J. & Munier-Jolain, N. (2009) Cutting and competition reduce weed growth: additive or interactive effects? '*XIIIème Colloque international sur la biologie des mauvaises herbes*, Dijon, France, p. 28-37.

5) Bienau, M., Meiss, H., Munier-Jolain, N. & Waldhardt, R. (2009) Contrasted weed seed banks in perennial and annual crops. Oral presentation by Miriam Bienau, *39th Ann. Conf. Ecological Society of Germany, Switzerland and Austria (GfÖ).* Bayreuth, Germany, p. 82.

6) Meiss, H., Médiène, S., Bienau, M., Waldhardt, R., Caneill, J. & Munier-Jolain, N. (2010) Diversifying crop rotations with perennial forage crops for integrated weed management. *15th European Weed Research Symposium*, 2010, Kaposvár, Hungary.

Posters

1) Meiss, H., Waldhardt, R., Gasquez, J., Bretagnolle, V., Munier-Jolain, N. & Caneill, J. (2007) Weed abundance may be reduced in crop rotations including temporary grasslands. *37th Ann. Conf. Ecological Society of Germany, Switzerland and Austria (GfÖ),* Marburg, Germany, p. 536.

2) Alignier A, Meiss H, Petit S & Reboud X (2008) Postdispersal weed seed predation ranged between 19 to 84% per week following a species preference rank. *24th German Conference on Weed Biology and Weed Control*, Hohenheim, Germany, p. 221-226.

3) Meiss, H., Naulin, C., Waldhardt, R., Caneill, J. & Munier-Jolain, N. (2008) Perennial crops and cutting frequency are important factors suppressing arable weeds in crop rotations. EURECO-GFÖ 'Biodiversity in an Ecosystem Context' – *11th European Ecological Conference of the European Ecological Federation* and *38th Ann. Conf. Ecological Society of Germany, Switzerland and Austria (GfÖ)*. Leipzig, Germany, p. 517.

4) Cordeau, S., Boursault, A. & Meiss, H. (2009) Sown field margin strips: What flora, what seed predators, what weed seed predation? *XIIIème Colloque international sur la biologie des mauvaises herbes*, Dijon, France, p. 50-59.

5) Meiss H., N. Munier-Jolain, J. Caneill, S. Médiène, V. Bretagnolle, R. Waldhardt (2010) Diversifying crop rotations with perennial forage crops: potential benefits for weed management & farmland biodiversity. *Gesellschaft für Ökologie* 40th Anniversary Meeting 'The future of biodiversity: Genes, Species, Ecosystems', Gießen, Germany, p. 308.

A GENERAL INTRODUCTION

A.I THE CHALLENGES OF SUSTAINABLE AGRICULTURE

Food production is one of the most essential human activities. The biggest part of food production is based on plants grown as crops that are directly eaten or fed to animals. Moreover, agriculture is the most important land use worldwide covering about 37% of the earth's land surface (Benton, 2007). The worldwide demand of crop products is strongly increasing due to both the growth of the human population and the changing human diets towards higher consumption of meat and milk products (Pingali, 2007). In 2050, global food demand is expected to increase by 50% compared to 2000 (Tilman *et al.*, 2001; Green *et al.*, 2005). In the past decades, agricultural production was able to follow the increasing demands, at least on the global scale. Global agricultural food production could *e.g.* be doubled from 1960 to 1995 (Tilman, 1999), leading even to periods of a global overproduction, although the problem of hunger could not be solved in many poor countries. Some of the increases in the global agricultural production can be attributed to a 12-18% increase in world cropland area, but the biggest part resulted from 'Green Revolution' technologies, including the use of chemical fertilizers, pesticides, high-yielding crop cultivars, mechanization and irrigation (Matson *et al.*, 1997; Tilman *et al.*, 2002; Foley *et al.*, 2005). The doubling of food production from 1960 to 1995 was associated with an about 7-fold increase in global nitrogen fertilization, a 3-4-fold increase in phosphorus fertilization, and a 1.7-2-fold increase in the surface of irrigated land (Tilman, 1999; Green *et al.*, 2005) and an 7-9-fold increase in the global pesticide use (WHO, 1990, p. 26; Green *et al.*, 2005).

These developments had various environmental and social impacts challenging the sustainability of modern agriculture. 'Over the past 50 years, humans have changed ecosystems more rapidly and extensively than in any comparable period of time in human history, largely to meet rapidly growing demands for food, fresh water, timber, fibre and fuel. This has resulted in a substantial and largely irreversible loss in the diversity of life on Earth' (MEA, 2005).

Agricultural practices may cause soil erosion, nutrients leaching or desertification deteriorating the soil resources for future farming (long-term profitability) and accelerating the euthrophication of terrestrial and aquatic ecosystems (Vitousek *et al.*, 1997; Csathó *et al.*,

2007). Agriculture is increasingly dependent on limited fossil resources to produce the fertilizer, pesticide and water inputs and to run the farming machinery. Pollution by pesticides and fertilizers may have negative effects on ecosystems and humans (Huber *et al.*, 2000). Agriculture is also an important driver of climate change. In 2004, it caused about 14% of the worldwide human greenhouse gas emissions (mainly CH_4 and N_2O), the 14% do not include the CO_2 emitted due to the use of fossil fuels (IPCC, 2007, Figure TS.2b). Land use change including the deforestation for agriculture accounted for an additional 17% of anthropogenic greenhouse gas emissions (mainly CO_2) in 2004 (IPCC, 2007, Figure TS.2b). It is estimated that soils of agricultural ecosystems have lost between 50% and 75% of their antecedent carbon content (Lal, 2007). Since 1850, about 35% of the anthropogenic CO_2 emissions resulted directly from land use (Foley *et al.*, 2005). Finally, land use change (including the conversion of natural areas and agricultural intensification) is thought to be the most important driver of the observed global biodiversity loss, even before climate change, nitrogen deposition and biotic exchange (invasions of exotic species) (Sala *et al.*, 2000). In Europe, both the intensification of farming practices as well as the abandonment of agriculture in other regions are both big threats to biodiversity at different levels (genes, species, ecosystems), including the 'wild' species typical for farmed landscapes (van Elsen and Günther, 1992; Matson *et al.*, 1997; Krebs *et al.*, 1999; MacDonald *et al.*, 2000a; Stoate *et al.*, 2001; Bretagnolle, 2004) and the domesticated species, varieties or races of crops and livestock. The loss of both 'wild' and 'domesticated' biodiversity (often also called 'associated biodiversity' and 'agrobiodiversity', respectively) may have various negative consequences. Besides aesthetic, moral and ethical/religious reasons, biodiversity is needed to maintain important ecosystem functions and services (reviewed in Chapin *et al.*, 2000; Hooper *et al.*, 2005; Diaz *et al.*, 2006). This includes nutriment cycling, pollination and pest control, thus also direct benefits for crop production (Altieri, 1999; Swift *et al.*, 2004; Clergue *et al.*, 2005; Berger *et al.*, 2006; Albrecht *et al.*, 2007; Moonen and Bàrberi, 2008). The chemical and genetic resources of many 'wild' organisms may also be used for the production of food or pharmaceutics and for crop and livestock breeding. Finally, there are more general benefits of biodiversity to human well-being, which are increasingly recognized (MEA, 2005; Diaz *et al.*, 2006).

The challenge of modern agriculture is thus to reduce its negative impacts on the environment and on biodiversity as well as the reliance on external inputs while maintaining or further increasing its productivity on the short and long term (Tilman *et al.*, 2002; Tybirk *et al.*,

2004). These aims are often considered contradictory, forming several trade-offs (Firbank, 2005; Green *et al.*, 2005): increasing the agricultural production would either require to expand the farmed area, implying further destruction of natural habitats, or to increase the farming intensity, implying to increase the use of external inputs (but see Badgley *et al.*, 2007). Inversely, some of the actions ('agri-environment schemes' Berger *et al.*, 2006) implemented to reduce or compensate the negative impacts of farming on the environment or on biodiversity, (also called 'wildlife friendly farming'), may reduce the per hectare crop production which may increase the pressure to expand the farmed land on natural areas (Green *et al.*, 2005).

A.II THE 'WEEDS TRADE-OFF'

Arable weeds and weed control play a central role in this conflict between (i) crop production, (ii) environmental protection and (iii) biodiversity conservation, which will be described in the following sections. For clarity, a definition and short discussion of the term 'weed' is given in Annexe 2.

A.II.1 Weeds & crop production

Weeds are frequently considered as one of the most serious factors threatening crop production. Crop yield loss caused by weeds is estimated at 10% on average worldwide (Oerke, 2006). Competition with the crop for growth resources (light, water, nutrients) is the most important factor (Caussanel, 1989; Zimdahl, 2004), but weeds may also have other negative effects such as the contamination of harvested grains by weed seeds, especially when crop and weed seeds have similar sizes, and mechanical crop harvest difficulties, especially for weed species with climbing morphologies such as *Galium aparine*. The presence of weed plants is also an important factor for the presence of animals and micro-organisms. This may include crop 'pests' such as aphids or slugs and crop diseases such as fungi developing on weed species that are taxonomically close to the crops (see e.g., Dulout *et al.*, 1997), but also 'auxiliary' organisms feeding on crop pests such as predatory carabids, rove beetles and spiders (*e.g.*, Schellhorn and Sork, 1997). For all these reasons, farmers try to keep weed densities low using different weed control techniques (see Ch. A.II.2 below). Weed scientist have intended to define theoretical 'economic thresholds' of weed densities above which the expected loss of crop yield or quality exceeds the costs of weed control (Coble and Mortensen, 1991), but this threshold concept was shown to be unsuitable for weed management for long-

term considerations (Munier-Jolain *et al.*, 2002). In reality, farmers have to control weeds not only to avoid yield losses in the current crop, but also to limit weed seed production for reducing weed infestations in future crops.

A.II.2 Weed control & environment

Since about 1950, herbicides have become the main technique of weed control in arable field crops (cereals, rape, beets, maize…) of industrialized cropping systems largely replacing other techniques and principles such as cultural and mechanical control (see Ch. A.III.2 below). Herbicides may be applied rather easily on large surfaces and are generally very efficient in killing the plants of most species. Therefore, herbicides may contribute to the maintenance of crop yields and to the economic profitability of the farms. The development of different herbicides was one important factor that enabled the simplification of cropping systems including shorter crop rotations and monocultures (and, more recently, no-till practices). However, the reliance on herbicides may have several agronomic, economic and environmental drawbacks that will be summarized in the following.

Efficiency and selectivity

Despite the intensive use of herbicides and other curative weed control techniques for many decades, the 'weed problem' could not be solved. Weeds did not disappear from arable fields, which was a widespread hope when herbicides became available. Intensified curative weed control as well as changed agronomic practices (including simplified crop rotations dominated by annual winter-sown crops) rather lead to reduced weed species numbers and community shifts. While many species showed strong population declines or even got extinct from entire regions (see Ch. A.II.3), some other less sensitive species showed increasing abundances and distributions. In some cases, the repeated use of herbicides with the same mode of action during many consecutive years selected herbicide resistant biotypes of weed species that are normally killed. Resistances are observed for an increasing number of herbicide molecules and weed species worldwide, but particularly in industrialized countries (as documented by Heap, 2009). In some situations, herbicides may also damage the crops and reduce crop yields which may lower the economic profitability. These problems of herbicide efficiency and selectivity show that weed management should not be based on one single principle.

Economic costs

Herbicides are relatively expensive; farmers in industrialized countries spend more money for herbicides than for any other pesticides. In 2006-2007, herbicides represented 64.4% of the US agrochemical market ($3914 out of $6077 million, AGROW, 2008) and 42.7% of the French marked (€787 out of €1841 million, UIPP, 2009). The high economic costs are the main reason why herbicides are much less used in poor countries.

Environmental pollution

Herbicides and their metabolites are frequently found in groundwater samples. Herbicides are the most widely used pesticides before fungicides and insecticides in terms of economic value (see above) and volume. In Germany, farmers bought more than 16,000 tonnes of herbicides in 2007, which corresponds to 51% of the total weight of pesticides bought (IVA, 2009), a proportion that may well be representative for other industrialized countries. Depending on soil characteristics and climatic conditions, some herbicide active ingredients may be rather quickly degraded by micro-organisms in the soil. Other herbicide types (including pre-emergence herbicides such as the triazines) are designed to stay active for longer times and are thus more frequently detected in groundwater samples (Arias-Estevez *et al.*, 2008). Moreover, herbicides are often applied before or shortly after crop sowing, when the soil is not covered by vegetation, and during wet periods when the risks of run-off and leaching are high.

In France, herbicides have been detected in 91% of 1690 observation points of surface water courses and in 55% of 846 groundwater observation points spread all over the metropolitan territory in 2005 (IFEN, 2007). Atrazine, which was officially banned in 2003 in France, showed only slightly decreasing concentrations from 1999 to 2007 in a catchment near Paris, and deethylatrazine, a metabolite of atrazine, showed no decreases at all during this time (Gutierrez and Baran, 2009).

Several active ingredients of herbicides or their metabolites may have negative environmental side effects (sometimes called ‘externalized ecological costs’). Herbicides may *e.g.* kill non-target plants and may indirectly affect many animals and micro-organisms by suppressing the plant species they depend on (see review by Freemark and Boutin, 1995; Hawes *et al.*, 2003; Gibbons *et al.*, 2006). Some herbicide active ingredients and adjuvant compounds may also have direct toxic effects to micro-organisms and animals but animal toxicity is mostly lower than for insecticides and fungicides, at least for the herbicides still authorized in the European Union. Even though evidence of direct toxicity of herbicides and adjuvant compounds to humans is limited (but see Benachour and Seéralini, 2008), herbicides are considered

problematic for the production of drinking water, and public authorities have established rules and targets for improving the quality of ground- and surface waters, such as the EU Water Framework Directive (Directive 2000/60/EC).

Due to these environmental, economic and agronomic problems and the possible impacts on human health, the reliance of crop production on herbicides should be reduced (Bastiaans *et al.*, 2000; Nazarko *et al.*, 2005; Blackshaw *et al.*, 2006). However, chemical weed control could not simply be substituted by other curative techniques such as mechanical or thermal weed control. These techniques may have reduced efficiencies, problems of selectivity and also high economic and ecological costs. For example, intensive soil tillage used as mechanical weed control may need a lot of labour time and energy, may damage the crops, increase soil erosion, nitrate and carbon losses and may also be detrimental to soil organisms (Stoate *et al.*, 2001).

A.II.3 Weeds & biodiversity

During the last decades, arable weeds showed very strong declines in abundances and diversity in many farming systems worldwide (Andreasen *et al.*, 1996; Sutcliffe and Kay, 2000; van Elsen, 2000). In the UK, where biodiversity-issues are well studied and published, farmland holds more scarce and threatened plant species than any other habitat (Rich and Woodruff, 1996), which may also be the case in many other countries. In France, about 42% of plant species richness has been lost during the last 30 years in arable fields in Côte-d'Or, a typical region of intensive agriculture (Fried *et al.*, 2009). This was probably due to changing agronomic practices including a) improvements in weed control, b) better crop seed cleaning techniques, c) the simplification of crop rotations including the strong reductions in spring sown crops and perennial crops and the specialisations of farms and regions to either arable crops or livestock farming, d) the use of more competitive crops (caused *inter alia* by higher fertilizer use), and e) the simplification of farmed landscapes including the increase in field size and removal of hedges and other non-crop elements (Robinson and Sutherland, 2002; Benton *et al.*, 2003; Gabriel *et al.*, 2005; Roschewitz *et al.*, 2005). Many studies showed that weed diversity is higher in more complex landscapes and in organically managed fields (see the reviews of Bengtsson *et al.*, 2005; Hole *et al.*, 2005; and Tscharntke *et al.*, 2005; and the study of Hotze and van Elsen, 2006).

Declines in weed diversity may have severe impacts on many other organisms (various types of animals and micro-organisms) that are using weeds either as hosts or food resources (Gerowitt *et al.*, 2003; Marshall *et al.*, 2003; Holland *et al.*, 2006; Storkey, 2006). Weeds may therefore be well suited as indicator organisms for farmland biodiversity in general (Albrecht, 2003). A large panel of different organisms may depend on weeds including herbivores, pollinators, seed eaters, and decomposers as well as organisms at higher trophic levels of many different taxonomic groups, *e.g.* arthropods (Norris and Kogan, 2005). Birds attracted the most attention. During the last decades, farmland birds showed dramatic populations decreases in many European countries (Krebs *et al.*, 1999; Bretagnolle, 2004; European Bird Census Council EBCC, 2008), which was much stronger than for any other group of birds (Fig. 1). Of the 195 bird species with an unfavourable conservation status in Europe, 116 are farmland birds (European Bird Census Council EBCC, 2008).

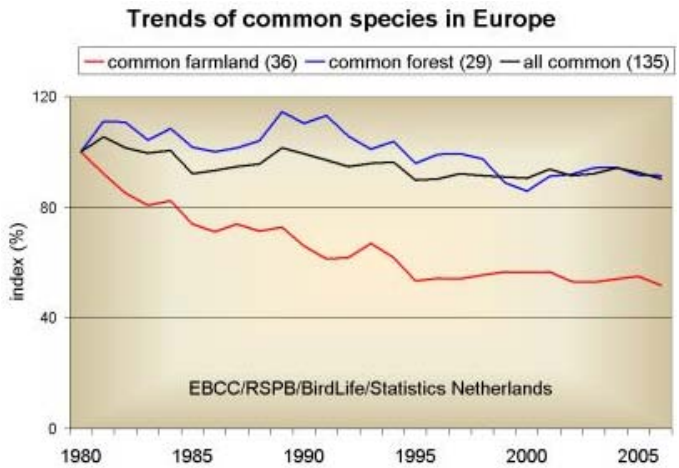

Fig. 1: Population trends of common bird species in Europe.

The graph (taken from the European Bird Census Council EBCC, 2008) shows an index of the average breeding population densities of 36 common farmland bird species (red line), which decreased by about 50% from 1980 to 2006, while all common birds (black line) and forest birds (blue line) declined by only 10%. Shown are weighted geometric means from 21 European countries (Austria, Belgium, Bulgaria, Czech Republic, Denmark, Estonia, Finland, France, Germany, Hungary, Ireland, Italy, Latvia, Netherlands, Norway, Poland, Portugal, Spain, Sweden, Switzerland, United Kingdom) that were compiled by the Pan-European Common Bird Monitoring Scheme (PECBMS), a common initiative of the EBCC, the Royal Society for the Protection of the Birds (RSBP), BirdLife International, and Statistics Netherlands.

These strong declines of farmland birds were probably caused by habitat destruction and food shortages linked to agricultural intensification (Fuller *et al.*, 1995; Siriwardena *et al.*, 2000;

Newton, 2004). Several bird species probably need both grasslands and arable crops for breeding and feeding and thus suffered from the loss of mixed farming and the geographical separation of crop and livestock production (Evans, 1996; Robinson *et al.*, 2001; Moreira *et al.*, 2005). Weeds and invertebrates are both very important in the diets of many farmland birds. Some birds probably suffered from a reduced presence of weed plants and invertebrates to feed their chicks in spring and summer. Moreover, weed seeds are particularly important for overwinter survival of adult farmland birds (Wilson *et al.*, 1999; Vickery *et al.*, 2001; Robinson and Sutherland, 2002; Hawes *et al.*, 2003; Marshall *et al.*, 2003; Holland *et al.*, 2006; Siriwardena *et al.*, 2006). Farmland birds clearly prefer fields with high weed seed densities as illustrated in Fig. 2.

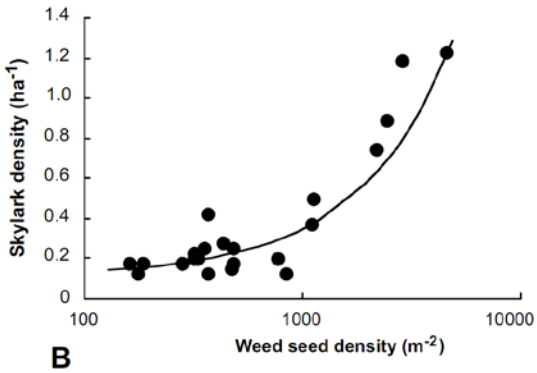

Fig. 2: Relation between weed seed density and skylark (*Alauda arvensis*) density in winter (Norfolk, UK). Figure reproduced with permission from Watkinson *et al.* (2000).

During the last century, the weed seed offer was probably strongly reduced due to steep reductions in weed seed bank densities (Robinson and Sutherland, 2002, see Fig. 3). Another important reason was probably the reduction of untilled stubble fields where weed seeds stay available on the soil surface during winter (Moorcroft *et al.*, 2002; Gillings *et al.*, 2005; Moreira *et al.*, 2005). The replacement of spring-sown crops by autumn-sown crops contributed to the decline in the areas of untilled stubble fields during winter.

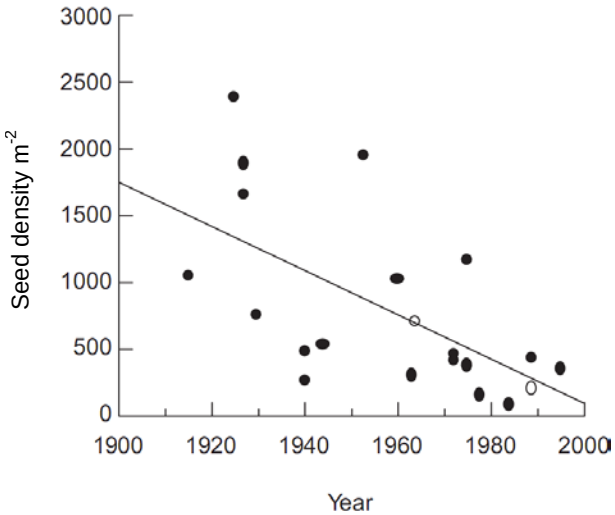

Fig. 3: Published estimations of superficial weed seed densities in arable soils during the 20th century.

The figure is reproduced with permission from a literature review by Robinson & Sutherland (2002). Points represent densities of dicotyledonous seed in the top 1 cm of soil in arable fields in Britain (filled symbols) and Denmark (open symbols). Studies were included only if they sampled the entire seed bank between September and November and if the fields had been part of a cereal-based rotation for at least 5 years; results from adjacent fields and years have been averaged.

While farmland biodiversity declines are best documented for the group of birds, many other animal groups including amphibians, reptiles, mammals and various invertebrates also showed reduced abundances and diversities which may often equally be linked to the reduced diversity of wild plants (see review by Robinson and Sutherland, 2002).

A.II.4 Summary

The section above has shown that (i) weed populations must be controlled to enable a high crop production, but that (ii) the concentration on chemical weed control is not sustainable due to widespread environmental pollution, possible impacts on human health, high economic costs and the risk of selecting herbicide resistances, and that (iii) weed abundance and diversity showed strong reductions due to modern farming practices, which had also detrimental effects on other elements of biodiversity and ecosystem functioning. This triple ‘weed trade-off’ must be solved to improve the sustainability of agriculture. However, there is probably no single solution to this complex problem.

A.III APPROACHES TO ALLEVIATE THE 'WEED TRADE-OFFS'

In this subchapter, several concepts and approaches will be exposed that might be useful to alleviate the trade-offs. Some of these concepts are rather well known and the reader will be referred to the corresponding literature, others will be explained in more detail, especially the integration of 'Perennial Forage Crops' (PFCs) into crop rotations. For instance, possible impacts of PFCs on weeds will be introduced in the following subchapter A.IV. Considering these different approaches, a modified cropping system will then be proposed and its potential for alleviating the weed trade-offs will be discussed in subchapter A.V. In view of the literature review about what is already known on the impacts of such perennial crops on weeds, subchapter A.VI will identify research needs and questions that will be addressed in this thesis.

A.III.1 Overview of the approaches

Alternative, non-chemical weed control techniques have often limited efficiencies. The use of a single alternative strategy might also cause the selection of 'resistant' weed biotypes in weed populations and tolerant species within the communities. Herbicides must thus be replaced by a combination of different techniques and changes in the cropping system to manage weed populations, as proposed by Integrated Weed Management (see Ch. A.III.2).

Moreover, simply replacing herbicides by another (non-chemical) weed control technique does not solve the trade-off with farmland biodiversity. Considerations and strategies how to alleviate this third part of the 'weed trade-off' started only very recently (Storkey and Westbury, 2007). This is a particularly difficult problem as there is certainly no 'ideal' weed infestation level and no optimum balance between production and biodiversity (Firbank, 2005). Farmers usually prefer to keep weed densities as low as possible, while they are required at certain densities to sustain populations at higher trophic levels. For example, Moorecroft *et al.* (2002) showed that linnets (*Carduelis cannabina*) and red buntings (*Emberiza schoeniclus*) only feed on fields where the densities of their dietary weed seeds exceeded 250m^{-2} on the soil surface, densities possibly problematic for crop production. However, weed species may differ both in their competitive ability and potential harm to crop production as well as in their 'biodiversity value' (support of other organisms) which might offer new possibilities for reducing the weed trade-off (see A.III.4 for more details). Another

approach may be to try to increase weed species diversity without increasing the total weed abundance (see A.III.3) or to try to promote weed seed predation (see A.III.5).

Two contrasting strategies will be shortly discussed in section A.III.6 that are frequently opposed in the literature: 'spatial separation of farming and biodiversity' *vs.* 'integrating of farming and biodiversityat the same place'. A promising 'third way' will be proposed in the following. This approach consists of a temporal separation of these different functions within the crop rotation, so that 'production' and 'conservation' phases of may form spatio-temporal mosaics at the landscape scale (see A.III.7). Crop rotation may diversify the selection pressures on wild organisms including weeds, animals and micro-organisms, which may have advantages both for crop protection and farmland biodiversity (A.III.8). Special attention will be paid to the diversification of crop rotations with perennial forage crops (PFC, also called 'temporary grasslands'), as they may differ in several important aspects to annual crops (see A.III.9).

A.III.2 Integrated Weed Management

Integrated Weed Management (IWM) emphasizes i) the combination of different preventive and curative weed management techniques and ii) integration of knowledge on the weed biology into the design of cropping systems (Gill and Holmes, 1997; Buhler *et al.*, 2000; Mortensen *et al.*, 2000; Buhler, 2002; Westerman *et al.*, 2005). IWM considers the causes of weed problems rather than only reacting to existing weed infestations. It may provide the farmer with a broader tool of techniques and principles that should diversify the selection pressures against weeds and hamper the selection of herbicide resistances. There are various cultural, physical, chemical, and biological techniques that may be used for integrated weed management (see also reviews by Mortensen *et al.*, 2000; Barberi, 2002; Buhler, 2002; Hatcher and Melander, 2003; Blackshaw *et al.*, 2006; Bastiaans *et al.*, 2008):

Long-term cropping system experiments showed that Integrated Weed Management can provide sufficient weed control and significantly reduce herbicide pollution (Chikowo *et al.*, 2009; Munier-Jolain *et al.*, 2009). But despite these good agronomic and environmental results in experiments, IWM is hardly introduced in real farms. Different factors may hamper their large-scale adoption including an increased system complexity and sometimes a reduced economic profitability (Leake, 1996; Bastiaans *et al.*, 2008; Pardo G *et al.*, in press). Today, IWM principles are probably mainly used in organic farming, where herbicides are forbidden

and higher production costs or eventually reduced crop yields may be compensated by higher marked prizes of the labelled products.

A.III.3 Combining high weed diversity with low weed abundance?

One strategy for alleviating the trade-off between the harms and functions of weeds might be the increase of weed species diversity without increasing the total weed abundance, thus increasing the evenness of the plant community. Higher plant diversity may increase the diversity of other trophic levels (animals and micro-organisms) as detailed in section A.II.3 above. However, weed abundance and weed diversity are generally positively related as both depend on the intensity of weed control. Hyvonen *et al.* (2003) observed always positive linear relationships when plotting the weed species richness against the number of weed individuals (both on logarithmic scales). However, the intercepts of these regressions were higher for organic cropping systems compared to conventional systems indicating that the abundance-diversity relationship may differ between cropping systems. At equal abundances, organic systems had about 2 more species compared to conventional systems. Such an improvement might be caused by the replacement of one dominating weed control technique that is very efficient on most weed species (*e.g.* herbicides with broad ranges) by several less efficient techniques and principles (IWM, see section A.III.2 above) or due to the rotation of dissimilar crops (see section A.III.8 below).

A.III.4 'Good' *vs.* 'bad' weeds?

Another approach goes beyond the former approach in considering differences between the weed species according to (i) their potential harm for crop production, (ii) their difficulty to be controlled and (iii) their role for biodiversity (habitat and trophic resource) and ecosystem functioning. Fig. 4 shows that weed species may considerably differ in 'harmfulness' (competitive ability) and 'biodiversity value' (number of associated insect species). But when combining these two criteria, many weed species are neither 'very good' nor 'very bad' but somehow intermediate.

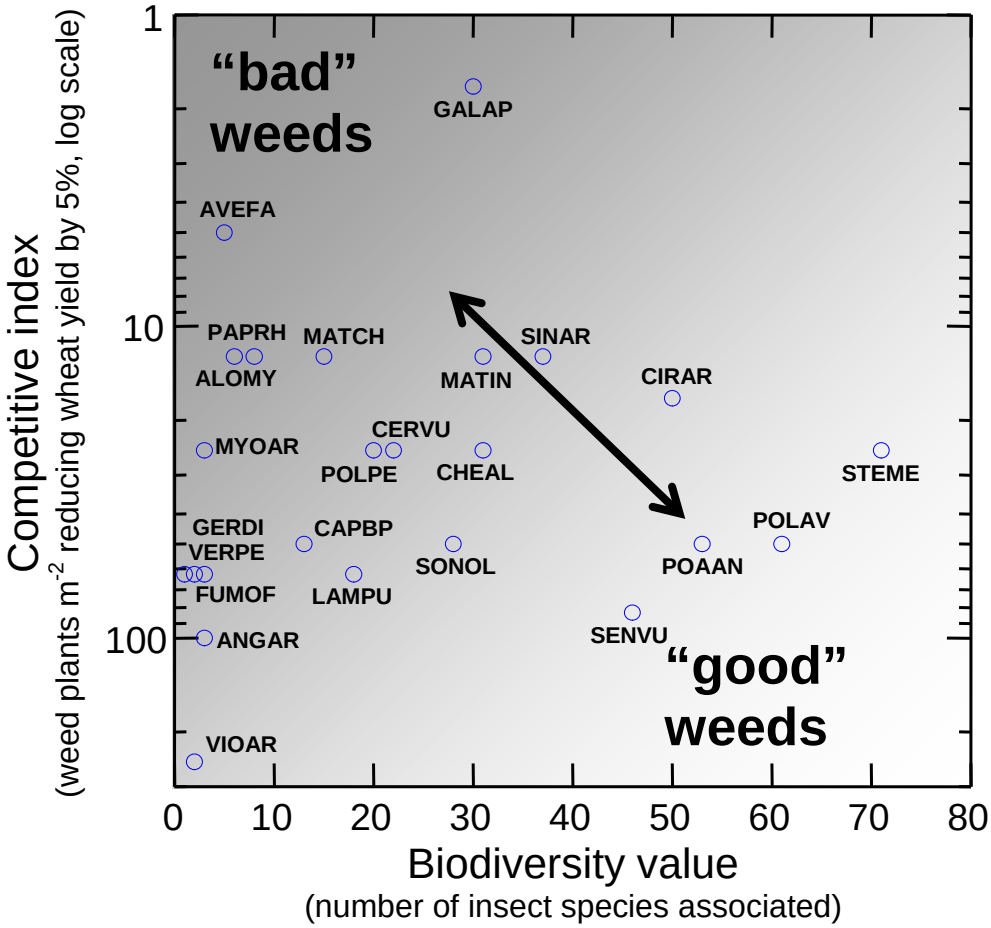

Fig. 4: Characterisation of common weed species according to their biodiversity value and potential crop yield loss.

The value for biodiversity is estimated by the number of insect species associated to the weed species in the UK, the potential crop yield loss is estimated by the density of weed plants per square meter reducing wheat yield by 5%. The raw data of this figure were taken from publications of Marshall *et al.* (2003) and Storkey (2006). See Annexe 3 for weed species codes.

Beyond this simple characterization of weed species based on these two criteria, Storkey (2006) used multivariate techniques to classify weed species into six 'functional groups' according to several morphological, physiological and phenological plant traits. He identified two groups of 'beneficial' weed species that combined a relatively low competitive ability with a high importance for invertebrates and birds.

One strategy for reconciling farming and biodiversity would thus be to selectively suppress the most harmful weed species while conserving species that combine high 'values' for biodiversity and least threat for crop production. First of all, this approach would need to establish knowledge both about (i) the harmfulness of each weed species to crops including

competitive yield loss (Cousens, 1985; Caussanel, 1989) and (ii) about the values of the different species for biodiversity and ecosystem functioning, which is a rather recent research area (Gerowitt *et al.*, 2003; Marshall *et al.*, 2003; Holland *et al.*, 2006; Storkey, 2006). However, both the harmfulness and the biodiversity values of weed species might differ between crops and regions and detailed knowledge is often lacking. The classification of weed species into more 'beneficial' and 'harmful' groups by Storkey (2006) are based on British data, classifications in other regions might differ. Moreover, indicators for biodiversity such as the number of associated insect species and the value of weed species for granivorous birds might underestimate the value of *e.g.*, rare weed species supporting endemic animals with very specific diets or habitat requirements or still unknown ecosystem functions and potential human uses. Second, strategies based on the distinct management of the most 'harmful' and the most 'valuable' weed species would require techniques that are able to selectively control the harmful species. Last but not least, it would need training of farmers and consultants to make them agree with the idea of 'protecting' a list of weed species in their own fields, whereas their current practices mostly aim at suppressing *all* wild species.

A.III.5 Favouring weed seed predation

One rather new approach to alleviate the 'weeds trade-off' may be the promotion of weed seed predation, *e.g.* the consumption of weed seeds by animals, which might alleviate the three problems of agriculture linked to weeds and thus create a 'win-win-win situation' (Table 2):

Table 2: Conceptual overview showing the central role of weeds in three big challenges of modern agriculture and the potential contribution of weed seed predation to solve these three 'weed problems'.

A) Challenges of modern agriculture	**B) Roles and conflicts of weeds**	**C) Potentials of weed seed predation**
1) Loss of biodiversity in farmlands must be stopped (functions, heritage,…)	1) weed diversity loss, → animal diversity loss,…	Energy for food chains (biodiversity)
2) Consumption of inputs must be reduced (pollution, natural resources, capital)	2) herbicides massively used for weed control	Reduction of weed seed densities (preventive weed control, economy of herbicides)
3) Agricultural production must be increased or stabilized (increasing demand)	3) weed control needed to prohibit crop yield loss (competition, contamination)	

Weed seed predation may increase farmland biodiversity as weed seeds constitute an important trophic resource for various animals such as birds, micro-mammals, beetles, ants, slugs, crickets, worms and even isopods, including several endangered species (Wilson *et al.*, 1999; Kollmann and Bassin, 2001; Saska, 2008). Compared to other plant tissues, seeds have relatively high energy contents and may be available during unfavourable seasons (winter) when other plant or insect food items are scarce (Wilson et al., 1999; Vickery et al., 2001; Holland et al., 2006). For the plant populations, seed predation may reduce the density of seed banks, hence the density of weed emergence in future crops, especially for annual weed species, which are entirely dependent on generative reproduction. This may be beneficial for crop production and may decrease the need for curative weed control such as herbicide applications. Several recent papers based on field experiments (Davis and Liebman, 2003; Westerman *et al.*, 2003c) and modelling (Jordan *et al.*, 1995; Davis *et al.*, 2004; Kauffman and Maron, 2006) suggest potentially strong impacts of seed predation on weed population demography. For example, Westerman *et al.* (2005) showed that a seed loss rate of 40% per year would be sufficient for stabilizing *Abutilon theophrasti* population densities in a system with low herbicide inputs. Weed seed predation may therefore be considered a 'biological weed control' (Hatcher and Melander, 2003; Westerman et al., 2005; , 2006).

A.III.6 Integration or spatial separation of farming and biodiversity?

Two strategies have been proposed for combining crop production and biodiversity conservation. 'Wildlife friendly farming' intends to integrate both at the same location whereas 'land sparing' intends to separate them spatially (Balmford *et al.*, 2005; Green *et al.*, 2005; Mattison and Norris, 2005). Green *et al.* (2005) argued that 'wildlife friendly farming' should be preferred if the relationship between productivity (crop yield) and biodiversity (wildlife population densities) is convex (high gain of biodiversity for small yield reductions). Conversely, 'land sparing' should be preferred if the relationship is concave (only small gains of biodiversity for the same yield reduction). However, the shape of this relationship is difficult to determine in practice.

In parallel to these theoretical considerations, both strategies may have several other advantages and shortcomings (summarized in Table 3). The 'land sparing' strategy may *e.g.* be more adapted to preserve natural areas with 'wild' habitats and associated plant and animal communities while 'wildlife friendly farming' may be more adapted for preserving typical farmland species and traditional cultural landscapes (van Elsen, 2000; Matson and Vitousek,

2006; Makowski *et al.*, 2007). Moreover, the highly productive regions or fields dedicated to crop production in the 'land sparing' strategy might be vulnerable to invasions of weeds, pests and diseases, and highly dependent on external inputs and as they are lacking mechanisms of auto-regulation such as predation and competition provided by established communities of plants, animals and micro-organisms and other ecosystem services provided by biodiversity. The regions or areas of intensive conventional agriculture may thus present various 'hidden environmental costs' and long-term risks (Vandermeer and Perfecto, 2005).

These two contrasting approaches of integration and spatial separation may both have important variations that are less considered in the literature. The 'land sparing' strategy may either consist of a separation between large nature reserves and highly productive regions where biodiversity and landscape diversity are largely eliminated (large-scale separation) or of rather small areas of non-crop habitats favourable to biodiversity [such as sown or natural field margin strips (Critchley *et al.*, 2006), hedgerows, small forests or ponds] within the landscape dominated by intensively farmed fields (small-scale separation, see illustration in Fig. 5 and details in Table 3). 'Wildlife friendly farming' may also be realized under various forms. However, it is usually thought to combine production and biodiversity at the same place *and time* (complete integration), which may be inefficient if the preservation of biodiversity requires high yield reductions, as pointed out by Green *et al.* (2005). However, there may also be an interesting and rarely considered variation of this strategy consisting in a *temporal separation* of the different functions.

A.III.7 Temporal separation of farming and biodiversity?

On the same field, periods of high yielding crop production may be alternated with phases favourable to different elements of farmland biodiversity at the scale of long crop rotations (see Fig. 5 for an illustration and Table 3 for further characteristics). The phases favourable to biodiversity may either consist of less intensive cropping (reduced inputs, reduced tillage, other crop types) or no production (such as rotational set-aside), or periods in between the harvest and the sowing of the next crop managed so as to favour biodiversity (such as overwinter stubble fields, OSFs) (Smith *et al.*, 1997; Moorcroft *et al.*, 2002; Critchley *et al.*, 2004). Many agri-environment schemes such as sown field margin strips are based on the spatial separation strategy and concern only a small fraction of land. This is probably one reason why positive effects on biodiversity are often limited (Kleijn *et al.*, 2006; Liira *et al.*, 2009). In contrast, actions implemented in the framework of the temporal separation may

concern whole fields and thus a larger proportion of the area, and may therefore have higher impacts on the environment, soil quality, and biodiversity. This is firstly important for organisms with low spatial dispersal abilities including soil micro-organisms, invertebrates and plants, but also for higher organisms such as a number of farmland birds, that rely on the provision of food resources on big surfaces and 'open' habitats (Siriwardena *et al.*, 2006; Storkey and Westbury, 2007). Modelling results from farming systems in the Netherlands indicated that rotating wildlife conservation practices across the farm (such as OSFs) is economically more efficient than fixed-location practices such as wildlife strips (Van Wenum et al., 2004).

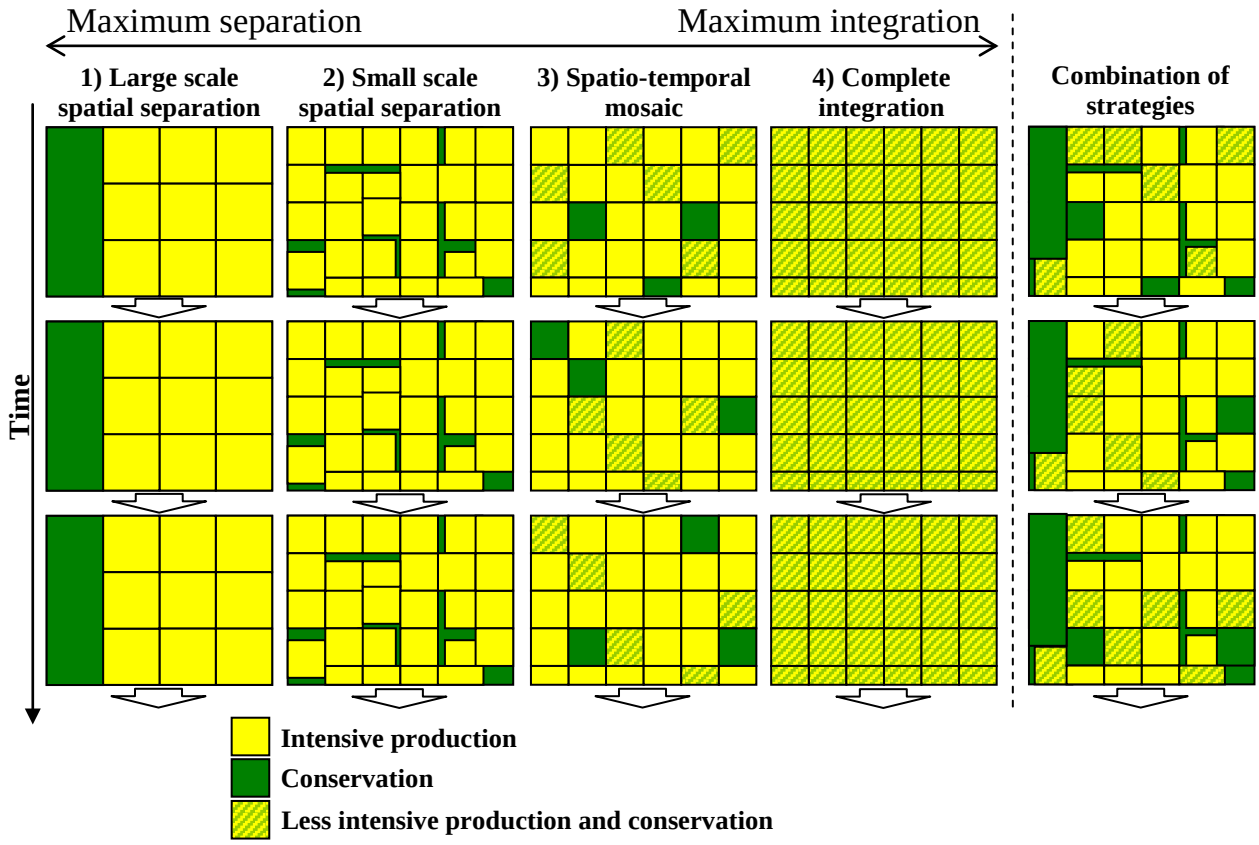

Fig. 5: Comparison of strategies for combining agricultural production and biodiversity conservation.
The four strategies on the left lie on a separation-integration gradient. In strategies 1 and 2, some parts of the land are intensively farmed while other parts are unfarmed nature reserves (large- and small-scale spatial separation, respectively). In strategies 3 and 4, all land is farmed, either always with a lower intensity in order to integrate biodiversity (strategy 4) or on a rotational scale forming a spatio-temporal mosaic of high, low and no crop production, as well as high and low values for biodiversity (strategy 3). See further descriptions in Table 3. The column of figures on the right shows a possible combination of the four strategies.

Table 3: Four strategies for combining agricultural production and biodiversity conservation.

The four strategies lie on a gradient between separation and integration, as illustrated in Fig. 5.

	'Spatial separation'		**'Wildlife friendly farming' (no spatial separation)**	
	1) Large-scale spatial separation:	**2) Small-scale spatial separation:**	**3) Temporal separation:**	**4) Complete integration:**
	Large 'untouched' nature reserves and regions of intensive production	Static mosaic of productive fields and 'unproductive' zones	Dynamic mosaic of high productive crops and less productive periods on crop rotation scale	Productive and unproductive organisms coexist at the same place and time
	← Separation			**Integration →**
What is pre-served?	Natural areas with associated 'wild' organisms	Some organisms typical for farmed landscapes (and some 'wild' organisms		Organisms typical for farmed landscapes, no space for 'wild' species
Fragmentation of habitats	Large-scale	Medium scale		Low
Use of eco-system services?	No	Some (needing spatial migration of organisms)	Some (needing spatial migration of org. or temporal outlast of positive effects)	Immediate, without spatial or temporal restrictions
Problems	No 'untouched' nature and no space for huge reserves in Europe	small size of protected areas		No optimal weed infestation level, no steady balance possible
Crop yield	Maximum on productive parts? But no production on 'spared' land		Spatio-temporal mosaic of high and low yield fields	Permanently reduced yield?
risk of weed, pest, disease invasions	High? (no mechanisms of auto-regulation)	?	?	Low?

A.III.8 Crop rotation

The main benefits of rotating different crops on a given field are (1) the maintenance of soil fertility and (2) the regulation of weeds, pests and diseases. Both may contribute to increase crop yields and reduce the need of inputs compared to monocultures (Smith *et al.*, 2008). Historically, the soil fertility has often been restored by letting the field lie fallow for about one year after 1-3 years of wheat, barley, oats or other cereal crops. In central and northern Europe, such 'food-feed-fallow' rotations were probably introduced by the Romans about 2000 years ago. Between about 1700 and 1800, European farmers gradually replaced the fallow phase by sown grass or legume forage crops that were grazed by livestock. They adopted four-year rotations including *e.g.* cereal grain crops, root crops and forage crops (Freyer, 2003). Fields were thus always planted for food or feed increasing the overall

productivity on the rotation scale. Moreover, the inclusion of a nitrogen-fixing legume crops contributed to increase the soil fertility.

The regulation of pests, weeds and diseases is the second reason why farmers use crop rotations instead of monocultures. The basic hypothesis is that each crop creates specific living conditions (ecological niches) determined both by characteristics of the crops (such as plant morphology, physiology and growth dynamics determining plant cover, microclimate and soil characteristics) and by the associated crop management practices (such as the types and dates of soil tillage, crop sowing, pesticide and fertilizer applications, irrigation and harvesting) (Doucet *et al.*, 1999). Crop plants and the associated management techniques act thus as biotic and abiotic 'filters' that determine the assembly of plant communities (Booth and Swanton, 2002). Therefore, some adapted weed species or ecotypes may develop and reproduce in a given crop situation, while many others cannot successfully terminate their life cycles. If the same or similar crop types are grown during several consecutive years on the same field ('monoculture'), the living conditions will be similar in every year. Such constant and predictable selection pressures could thus favour some adapted species, whose populations may thus steadily increase and reduce the yield or quality of the crop. At the same time, all other species are likely to decline or disappear reducing biodiversity. In contrast, alternating different crop types and different associated management practices on the same field would provide different selection pressures in every year, hence (i) avoiding continuous population increases of single adapted species but also (ii) increasing the species diversity. This would correspond to the 'diversity begets diversity'-hypothesis introduced by Whittaker (cited in Palmer and Maurer, 1997). Crop rotation may thus also be favourable to biodiversity, which would be a third function.

The importance of crop rotations decreased after World War II. Its main agronomic functions could be replaced by mineral fertilizers and synthetic herbicides, fungicides and pesticides and farming machinery (Peoples *et al.*, 1995; Stoate *et al.*, 2001). Other reasons probably included the globalization of agricultural markets leading to a specialization of farms and regions to some kind of products and public subsidies favouring some crops types more than others (Liebman *et al.*, 2008). Today, conventional cropping systems use rather simple rotations or loose successions of 2-3 annual cash crops (or even monocultures) of the economically most profitable crops. Such short and simple crop rotations may provide only limited benefits for weed management and biodiversity and these benefits may be only visible in low-input systems (Barberi *et al.*, 1997; Smith and Gross, 2006). The (re-)diversification of crop

rotations is thus an obvious approach to reduce the 'weeds trade-off', *i.e.* to combine high crop yields, low reliance on pesticide and fertilizer inputs and high biodiversity (see Fig. 6).

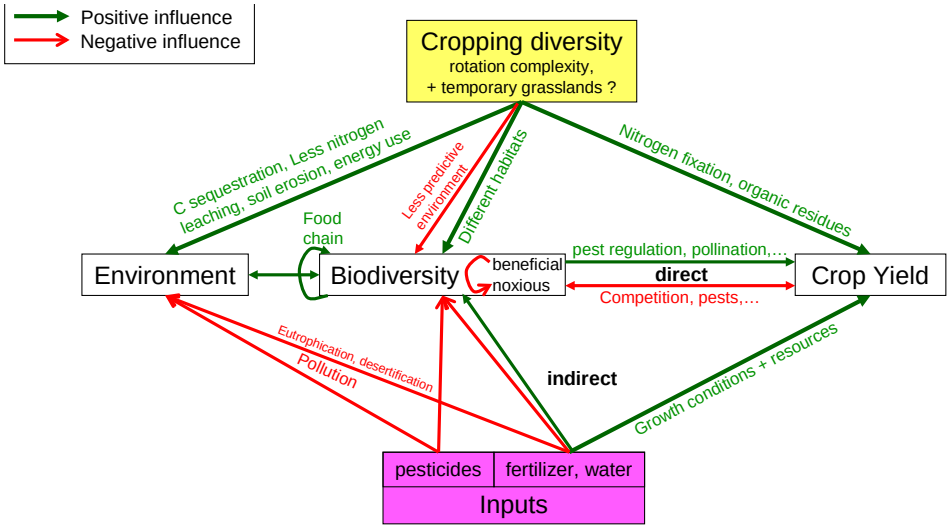

Fig. 6: Simplified illustration of the trade-off between farming (crop yield), environmental protection and biodiversity conservation.

The trade-off is mediated by influences of the farming inputs (pesticides, fertilizers and irrigation water) (positive for crops, negative for environment and biodiversity). By increasing the crop diversity (using complex crop rotations), some of the functions of the farming inputs (crop fertilisation, pest regulation) may be substituted, which would have different beneficial effects on the environment and biodiversity.

The present work focalizes on the temporal diversity of crops in the framework of crop rotations. Growing several crop species together at the same time ('intercrops', 'companion crops' and 'undersowing' techniques) is another possibility to increase the crop diversity. It may also be used for Integrated Weed Management and for increasing biodiversity in the farmland (Liebman and Dyck, 1993; Palmer and Maurer, 1997) but will not be addressed in this work.

Crop rotations may be diversified by introducing either (a) other annual 'cash' crops, preferably with dissimilar characteristics, (b) 'cover' or 'catch' crops grown between successive annual crops (replacing periods of bare soil) (Barberi, 2002; Smith and Gross, 2007), but also (c) perennial crops that last for several years on the field (Sebillotte, 1980; Freyer, 2003) (see section A.III.9). Perennial crops may be of special interest for weed management and biodiversity, as it may provide conditions for weeds (and animals) that are

very dissimilar to annual crops, and other benefits to biodiversity, environment and crop production.

A.III.9 Perennial forage crops (PFCs)

PFCs may consist of various perennial legume species such as lucerne/alfalfa (*Medicago sativa*), different clovers (*Trifolium sp.*), and several other legume species (Fabaceae family), as well as different grasses such as *Dactylis glomerata*, *Festuca sp*., *Lolium sp*., *Phleum pratens*, and *Poa pratensis.* They are often sown as legume-grass mixtures (Freyer, 2003). Such crops are habitually used for livestock forage production in mixed farming systems (mown for hay or silage or grazed as pasture) (Summers, 1998; Sulc and Tracy, 2007). In contrast to all annual crops, such crops last on the field for more than one year, typically about 2-5 years, sometimes even longer. They may thus be seen as intermediate between annual crops and permanent grasslands or pastures. In the literature, they are referred to with various names including 'temporary grassland' (TG), 'artificial grasslands', 'pluriannual crop', 'ley crop', 'sod crop', 'fodder crop', 'hay crop' or even 'cleaning crop'. Since 1700, sown PFCs substituted the fallow phase of crop rotations in 'alternate husbandry' systems (see A.III.8). Both phases may increase soil fertility after depletion by annual crops and disrupt the cycle of diseases, pests and weeds (Freyer, 2003).

During the last 40 years, such 'mixed' crop–livestock farming systems have declined, especially in intensive conventional farming systems, while PFCs remained more frequent in organic and integrated systems (Freyer, 2003). In France, the area of temporary grasslands was reduced from $1.5*10^6$ ha in 1970 to $1.1*10^6$ ha in 2000 (-25%), while the surface of all annual crops was strongly increased from $12.2*10^6$ ha to $15.2*10^6$ ha (+25%) during the same period (Bisault, 2008). Major reasons for this decline include

i) the splitting of cereal and livestock production to different farms and different regions,

ii) the substitution of grass- or roughage-based forages by grain-based forages in intensive livestock production systems,

iii) the availability of tractors replacing draught animals that needed an on-farm forage production, and

iv) the availability of cheap and efficient mineral fertilizers, herbicides and pesticides that substituted some of the beneficial effects of perennial crops on the following annual crops (Entz *et al.*, 2002; Katsvairo *et al.*, 2006b).

A.IV EXPECTED IMPACTS OF PERENNIAL CROPS ON WEEDS

A.IV.1 Literature review

Empirical studies investigating the impacts of perennial crops on arable weeds are very heterogeneous in terms of methodology and not so frequent, probably as the importance of this crop type decreased during the 20th century. In this review, studies were found mainly by using the following key words in popular search engines such as the 'ISI web of knowledge' (www.isiknowledge.com) and 'Google Scholar' (http://scholar.google.com): "crop rotation", "temporary grassland", "forage", "fodder", "ley", "mixed farming", "alfalfa", "lucerne", "clover", "legume-grass mixture", "weed management", "weed community", "crop protection" and by searching both the references cited in these studies and younger articles citing them. The review was limited to cropping systems in temperate climates and to papers published after 1992, thus not included in the review of Liebman & Dyck (1993).

There are numerous studies comparing weed infestations in different crop rotations. However, most studies include only annual crops. This may also be illustrated by the fact that 26 out of 29 comparisons between rotations and monocultures reviewed by Liebman & Dyck (1993), crop rotations included only annual crops. In the literature search, 15 more recent studies reporting impacts of PFCs on weeds (sometimes described by several successive publications) were retained. These studies will be shortly reviewed in the following (see also the summary in Table 1 of Article 1). 13 studies were based on field experiments, only one study on a weed survey covering a large number of fields of a whole region and one study on interviews of farmers.

A.IV.1.1 Farmers interview

Entz *et al.* (1995) interviewed 253 farmers known to include forages in their crop rotations in two regions of Canada, Manitoba and Saskatchewan in 1992. 67% of them reported yield benefits and 83 % weed control benefits from including forages in their rotations. Weed control benefits lasted for one (11% of respondents), two (50% of respondents), or more (33%

of respondents) years after forages. Forage crops mostly lasted between 3 and 9 years on the fields. This duration mainly depended on forage yield, only 12% of the farmers adjusted it to maximize rotational benefits (Entz *et al.*, 1995).

A.IV.1.2 Regional weed survey

Ominski *et al.* (1994; , 1999) compared the weed communities in i) 63 cereal fields following 3-6 year old alfalfa stands and ii) 54 cereal fields following at least 5 years of annual cereal grain crops. Cereals after alfalfa were characterized by lower densities of *Avena fatua*, *Brassica kaber*, *Cirsium arvense*, and *Galium aparine*, higher densities of *Taraxacum officinale* and *Thlaspi arvense* while *Amaranthus retroflexus*, *Chenopodium album*, *Polygonum convolvulus*, and *Setaria viridis* had no consistent or no significant differences.

A.IV.1.3 Field experiments

The largest experimental study was done by Andersson & Milberg (1996; , 1998) on 3 sites in southern Sweden. They compared 4 nitrogen application rates and three 6-year rotations comprising either (i) a 2-yr grass ley, (ii) a 2-yr legume-grass ley, or (iii) spring wheat followed by a repeatedly harrowed fallow applied since 26-30 years. These 2years phases were always followed by winter turnip rape, winter wheat, oats and barley, which was undersown in the two ley rotations. The weed communities differed strongly between the sites and the crops (highest in turnip rape) but did not differ consistently between the fertilisation and rotation treatments and none of the three rotations developed any major weed problems.

Norris & Ayres (1991) observed that yellow foxtail [*Setaria glauca* (L.) Beauv.] invasion was lowest when alfalfa was cut with an 37-days interval, intermediate for a 31-day interval and highest for a 21-day interval. In two out of three years, delaying the irrigation (14 days instead of 7 days after cutting) further reduced *S. glauca* density. While yields increased with the cutting interval, economic return was best for the intermediate 31-day cutting interval due to lower forage quality with the 37-day interval.

Gill & Holmes (1997) reported that some farmers in southern Australia include a 2-3 years pasture phase into crop rotations to manage herbicide resistant ryegrass (*Lolium rigidum*) and *Avena fatua*. A review of several small field experiments in southern Australia indicated that a combination of grazing by sheep, cutting and other IWM techniques can successfully deplete the seed bank of problematic *Lolium* weeds.

Clay & Aguilar (1998) compared the weed seed banks, weed biomass and corn yields after (i) continuous corn or (ii) corn grown after 2-year-alfalfa stands with three fertilizer and herbicide input levels in South Dakota, USA. Alfalfa had positive impacts on corn yields and weed control, especially for the low and intermediate input systems.

Schoofs & Entz (2000) compared the weed suppressive potential of five different spring seeded one-year forage crops followed by a pea (*Pisium sativum* L.) test crop. All forage systems were at least as effective as a sprayed wheat (*Triticum aestivum* L.) control in suppressing *Avena fatua* L. and sometimes *Setaria viridis* L. Beauv. grass weeds; however, effects on broadleaved weeds were variable, especially for systems that did not provide season-long competition. In general, one-year forage crops showed significant weed control benefits, but benefits of pluriannual forage crops reported by the same research team (Entz *et al.*, 1995) were stronger. The effectiveness of the different grain and forage crops to reduce weed seed production ranked as following: fall rye (*Secale cereale* L.) (grain crop) > winter triticale (*Triticosecale*) (simulated grazing) > spring/winter triticale intercrop (silage, then simulated grazing) > sorghum-sudangrass (*Sorghum bicolour* [L.] Moench × *Sorghum sudanese* [Piper]) (hay) = alfalfa (hay) > spring triticale (silage) = weed fallow (silage) = sweet clover (*Melilotus officinalis* L.)/winter triticale double crop (hay, then simulated grazing) > wheat grain crops with three different herbicide regimes.

Sjursen (2001) monitored the development of weed densities in the seed bank and the emerged vegetation in organic 6-year rotations including 3-year periods of perennial grass-clover leys and a sequence of three annual crops. Seed densities of dicotyledonous weed species were highest after the 3 annual crops (about 17600 seeds m^{-2}) and lowest after the ley periods (7200 seeds m^{-2}), indicating a reduced seed input during the ley periods. In the emerged vegetation, species richness decreased from 19-20 during the annual crops to 8 in the third year ley crop while it remained constant in the seed bank (18-21 species). However, correlations between seed bank and emerged weed densities were rarely significant limiting the potential for predicting the actual weed vegetation.

Cardina *et al.* (2002a) and Sosnoskie *et al.* (2006) compared the weed seed density, diversity, and community composition between three crop rotations: continuous corn (CCC), corn-soybean (CS), corn-oat-hay (COH) and three tillage systems (conventional, minimum, and no-tillage) that were applied in two 35-year field experiments in Ohio, USA. Crop rotation was a more important determinant of weed seed density and species composition than tillage system.

On average, the 3-year rotations had highest total weed seed densities and species diversities, probably due to the strongly reduced herbicide inputs and diversified crop sowing dates in this system, while the plant communities in continuous corn had lowest species diversity and evenness (high abundances prevalence of single weed species such as *C. album*) and grasses were more frequent in the rotations including hay crops. Moreover, several interactions between the rotation and tillage treatments were significant.

Bellinder *et al.* (2004) compared the weed seed banks before and after four 2-year crop rotations including alfalfa, clover (*Trifolium pratense* L.), rye (*Secale cereale* L.), and sweet corn (*Zea mays* L. var. *rugosa* Bonaf.) with a rye cover crop at three sites in New York, USA. Weed seed banks increased in all four systems. Increases were highest in rye, while seed bank densities did not differ between the two mown forage crops and corn, although pre- and post emergence herbicides and soil tillage (disking) was used only in corn.

Teasdale *et al.* (2004) and Cavigelli *et al.* (2008) compared the weed seed banks during 6 years between three crop rotations: (i) a 2-year corn (*Zea mays* L.)–soybean [*Glycine max* (L.) Merr.] rotation, (ii) a 3-year corn–soybean–wheat (*Triticum aestivum* L.) rotation, and (iii) a 4+-year corn–soybean–wheat–red clover + cocksfoot (*Trifolium pratense* L. + *Dactylis glomerata* L.) hay rotation. Annual dicotyledonous species including *Amaranthus hybridus* L. and *C. album*, the most harmful weeds in these systems, showed reduced seed bank densities after the hay phase while some annual grasses showed the opposite effect. The weed suppressive effects were strongest when the 4-year rotations started with hay crops.

Stevenson *et al.* (1997; , 1998) found greater weed species diversity in a barley/forage rotation compared to a barley monoculture. The barley-forage rotation showed increase in barley dry weight seed yield (+ 29% and + 26% compared to the monoculture) in all years except one, despite greater weed pressure in the barley-forage rotation, suggesting benefits of forages to subsequent annual crops.

Albrecht (2005) analyzed the weed seed banks during 8 years on a farm recently converted to organic practices in Bavaria, Germany. On average, rotated grass-clover forage crops (undersown in winter cereals, lasting 1.5 years) reduced the seed bank density by 39%, winter cereals (wheat or rye, *Secale cereale* L.), sunflowers (*Helianthus annuus* L.) and lupins (*Lupinus albus* L.) increased it by 30-40% per year and potatoes (*Solanum tuberosum* L.) and sown fallows caused no significant changes.

Heggenstaller & Liebman (2006) compared a conventionally managed 2-year rotation (maize–soybean), a 3-year rotation (maize–soybean–triticale undersown with red clover) and a 4-year (maize–soybean–triticale undersown with lucerne–lucerne). The 3-year and 4-year rotations were managed with 72% and 79% less herbicides than the 2-year rotation, respectively. Weed populations profited from the herbicide reductions in the 3- and 4-year rotations but increases of *Abutilon theophrasti* could be prevented due to low fecundity in triticale and low seedling survival and fecundity in lucerne. In contrast, results for *Setaria faberi* were more heterogeneous leading to population increases in some years.

Hiltbrunner *et al.* (2008) studied weed dynamics and diversities in 15-years field experiments in Switzerland including winter wheat, maize, summer or winter barley, potatoes or oilseed rape and temporary grassland in organic, integrated and conventional cropping systems. In the organic systems, the diversification of crop rotations with temporary grasslands was an important factor keeping weed pressure low, however, some species such as *Taraxacum officinale* and *Rumex obustifolius* showed increasing tendencies in the perennial crops and dominated the weed community in the following annual crops.

A.IV.1.4 Discussion and limits of the reviewed studies

Most of the reviewed studies indicated that PFCs have negative effects on some weed species and positive effects on others (see also the species listed in Table 1 of Article 1). This indicates that PFCs basically tend to change the weed community composition.

The generality of these findings may however be limited as most of the reviewed studies (i) were based on field experiments conducted on one or few experimental sites, (ii) involved rather short duration of forage crops (1-2 years) inserted in rather short experimental rotations (2-4 years) and (iii) often focused on one or few locally important weed species. The only two exceptions are the farmer interviews (Entz *et al.*, 1995) and the weed surveys (Ominski *et al.*, 1999) which were both done in the same region in Canada (see above). These studies might be closer to reality, where forage crops last often for more than 2 years on the fields and farmers often do not apply fixed rotations as in the experiments but adjust their crop sequences and forage crop duration depending on various economic and agronomic factors.

One mean for increasing the generality of experimental results is to understand the underlying mechanisms. Unfortunately, most reviewed studies did not give many details on the mechanisms causing the impacts on weeds. Authors observing reduced weed abundances after

forage crops sometimes cited the increased competition or the mowing or grazing activities as possible causes (*e.g.*, Norris and Ayres, 1991; Schoofs and Entz, 2000), while increased abundances were sometimes linked to reduced herbicide use or reduced soil tillage (e.g., Cardina *et al.*, 2002a; Bellinder *et al.*, 2004). Few details were given for identifying which phases of the weed life cycle were mostly affected by PFCs. Only Heggenstaller and Liebman (2006) showed that alfalfa reduced the seedling survival and fecundity of *Abutilon theophrasti*, the most important weed species in their system.

A.IV.2 Hypothetical mechanisms causing the impacts

Annual and perennial crops differ in several important aspects concerning both the characteristics of the crop plants and the crop management, including weed control actions (see also Table 4). The impacts of PFCs on arable weeds might therefore be caused by various mechanisms.

1) PFCs are characterized by the absence of soil tillage during the whole duration of the crop (about 2-6 years), thus often much longer than with annual crops, where soil tillage and sowing operations are mostly effectuated once or even several times per year. This may have various impacts on weeds such as a reduced germination of weed species needing light or oxygen stimulus for germination (Huarte and Arnold, 2003) and an increased survivorship of established weed plants.

2) In contrast to these reduced soil disturbances, mowing or grazing may lead to frequent mechanical disturbances of the aboveground vegetation. While most annual crops are harvested only once per year, forage crop cutting is effectuated about 2-5 times per year, thus often both at earlier and later times of the year compared to the single harvesting date of annual crops. This may reduce the survivorship, biomass and seed production of weeds (Gill and Holmes, 1997), although species may strongly differ in their sensitivity to cutting.

3) PFCs are often characterized by strong canopy closures and deep and dense rooting systems. This may cause intense competition against weeds. Compared to annual crops, competition may not only be stronger, but also more extended in time. While annual crops are often characterized by periods of weak competition (i) during crop establishment, (ii) crop ripening/senescence and (iii) after harvest, perennial crops have only one establishment phase in the first year and regrowth after cutting may be faster than initial

growth of any (crop or weed) plant leading to temporarily extended vegetation cover and competition against weeds. However, older perennial crop stands may show higher spatial heterogeneities and 'gaps' that may be occupied by weeds. The vigour of the perennial crops may decrease with time due to plant senescence and mortality, which is often the reason to terminate the perennial crop stand (Entz *et al.*, 1995).

4) Herbicide use is often lower in PFCs as compared to annual crops, or even completely absent as in organic systems. In most cases, herbicides are only occasionally used during the establishment phase and sometimes for stand termination. Herbicide use reductions may be possible as the weeds are suppressed due to the other mechanisms listed here or by alternative non-chemical weed control techniques adapted to perennial crops (Summers, 1998). Several weed species may also be tolerated in forage crops, as they may have good forage values, while other weed species such as *Rumex crispus* L., and *Conyza canadensis* (L.) Cronc. may be rejected by livestock or may even be toxic such as *Senecio vulgaris* L. (Summers, 1998). Reduced herbicide use in the perennial crops may especially benefit all plant species with high herbicide sensitivities.

5) Fertilization and irrigation schemes in PFCs may also differ from annual crops. Nitrogen fertilization is often reduced or absent thanks to nitrogen-fixing legume crop species. Irrigation may be less necessary than for annual crops due to the deep roots of many perennial crops. Both modifications may reduce weed growth and seed production.

Table 4: Characteristics of annual crops and PFCs with possible impacts on weeds.
(Further indirect effects are marked in the main text).

	Annual grain crops	**Perennial forage crops**	
			Potential effects on weeds
1) Belowground disturbances:	Soil tillage and sowing operations at least once per year, often more frequently, sometimes additional cultivation for mechanical weed control	No soil disturbance throughout the whole duration of the crop (2-6 years), accumulation of plant debris on the soil surface (mulch)	Reduced seed germination [lacking tillage stimulus, (Huarte and Arnold, 2003), mulch], increased plant survivorship (no physical damage)
2) Aboveground disturbances:	Mostly one cutting per year for crop harvest	Frequent cuttings (2-5 per year) (forage harvest)	Reduced plant survival, reduced seed production (damage of plant canopies) (Gill and Holmes, 1997)
3) Crop competition:	High only during some seasons of the year (weak after sowing, at crop senescence and absent after crop harvest)	High during the whole vegetation period due to deep and dense rooting systems and intense canopy closures, except during the establishment phase and directly after cuttings	Reduced germination, growth and reproduction (limiting growth resources) (Schoofs and Entz, 2000)

4) Herbicide use	Normal herbicide use	Lower than in annual crops or completely absent	Increased weed plant survivorship and seed production
5) Fertilisation	Use of mineral N-fertilizer	Symbiotic fixation of atmospheric N	Delayed N-availability may favour crops over small-seeded weeds (Liebman and Ohno, 1998; Liebman and Davis, 2000).

Besides these different direct effects on weeds, the differences between annual and perennial crops may also have several indirect effects, involving *e.g.* modified microclimate and soil characteristics resulting from the permanent vegetation cover and the absence of soil tillage in perennial crops (Entz *et al.*, 2002). Weeds might also be affected by allelopathic compounds released by some perennial crop species including alfalfa (Xuan *et al.*, 2004; Khanh *et al.*, 2005) and clover (Liebman and Ohno, 1998; Ohno *et al.*, 2000). Such phytotoxic effects may be stronger for weeds than for crops, which may be caused by the small seed size of most arable weeds compared to crops (Liebman and Davis, 2000). Due to increases of soil fertility (organic matter and nitrogen fixation) during the perennial crops, mineral fertilisation may also be reduced in the following annual crops. This may lead to a delayed N-availability compared to mineral fertilizer application, which may also give an advantage to big seeded crops over small seeded weeds (Liebman and Ohno, 1998; Liebman and Davis, 2000). Indirect impacts on weeds may also arise if the crop plants grown after PFCs show a more vigorous and competitive growth due to a better soil structure and fertility or lower pest and pathogen pressures than after annual crops. Finally, indirect impacts may also be caused through interactions with animals and micro-organisms that find a modified habitat in perennial crops. One hypothesis would be that organisms feeding on weed seeds (seed predators) find better habitat conditions in perennial crops which may cause higher weed seed mortality compared to annual crops (Westerman *et al.*, 2005; Heggenstaller *et al.*, 2006).

All these different hypothetical impacts of PFCs may strongly differ between weed species according to their morphological, physiological and phonological traits (MPP-traits, Violle *et al.*, 2007). PFCs may thus provoke weed community shifts suppressing some species and favouring others. Weed species that are best adapted to annual arable crops (including the most noxious ones) would be rather disfavoured while other species less or not occurring in annual crops would profit. In this case, the integration of perennial crops in arable crop rotations would reduce the weed pressure in the following annual crops and thus allow a high yielding crop production with fewer inputs.

A.V DIVERSIFIED CROPPING SYSTEM CONCEPT

A diversified cropping system is proposed to alleviate the 'weeds trade-off' described in section A.II. This system is intended to modify 'conventional' cropping systems of industrialized countries dominated by short crop rotations or monocultures of annual cash crops (*e.g.* cereals, rapes, maize, beets), by combining several of the elements introduced in the preceding section A.III. This concept is based on the 'temporal separation' strategy (section A.III.7) involving a long crop rotation comprising **three phases**:

1) periods (several years) of high yielding annual cash crops (production function),

2) periods (several month) favourable to different elements of farmland biodiversity and the physical environment such as over-winter stubble fields (followed by spring or summer sown crops), rotational set-asides, or other appropriate 'agro-environment schemes' concerning the whole field, and

3) periods of pluriannual crops (such as PFCs, *c.f.* section A.III.9, forage or biomass production) that may have a regulating function on weed populations adapted to annual crops (weed regulation function, detailed in section A.IV above) and may also be favourable to the environment (see section A.V.3 below) and several components of farmland biodiversity (see section A.V.2 below).

An exemplary crop rotation including these three phases is illustrated in the upper part of Fig. 7. On the landscape scale, the three periods should form a dynamic mosaic (*c.f.* section A.III.7 and Fig. 5). During the annual crop phase (1), curative weed control would be reduced, especially the use of herbicides, to limit their different draw-backs (c.*f.* section A.II.2). Weeds are primarily managed by a combination of alternative preventive and curative techniques in the framework of Integrated Weed Management (IWM, see A.III.2). Herbicides should only be used if other IWM-techniques are not sufficient. Herbicide application is thus limited to some years and some crops, which should also reduce the risk of selecting resistant weed biotypes. Moreover, farmers should prefer herbicide types (a) with narrow spectra targeting mainly problematic weed species that can not be well controlled by other means, (b) with low toxicity to other organisms and (c) quick degradation.

The modified system based on such a spatio-temporal separation of different agro-ecological functions may have strong impacts on weeds (see section A.IV above), but also on other elements of farmland biodiversity, the physical environment and crop yields & economic

profitability, which will be summarized in the following sections A.V.2 - A.V.4. Table 5 shows an overview of these possible impacts.

Table 5: Overview of expected impacts of the proposed modified cropping system.
Impacts of the three modifications and the resulting increased spatio-temporal landscape heterogeneity are detailed on plants, animals & micro-organisms, the physical environment and crop production. References will be found in the main text. This thesis concentrates on the impacts of PFCs on weeds (shaded in grey).

Modification	Expected impacts on…			
	Plants/weeds	**animals & micro-organisms**	**physical environment**	**crop production**
1) replacement of herbicides by IWM-techniques in annual cash crops	Stable or increased abundances (if alternative techniques are less efficient), increased diversity	Increased abundance and diversity: less direct toxic effects and positive indirect effects (plants as habitat and food)	Reduced pollution by herbicides, more erosion and leaching if intensive soil tillage	Similar if correct weed control, no 'phototoxic' effects of herbicides
2) Introduction of OSFs	increased seed production (no disturbance), but also seed mortality (seeds remain at the surface)	Improved habitat and food availability	Less erosion and leaching than tilled soil	Establishment of following crop may be more difficult
3) Introduction of PFCs	Plant community shifts (main hypothesis of this work)	More stable habitat, more abundant food resources due to reduced soil disturbance, permanent vegetation	More water infiltration, less erosion and leaching, more organic matter, N-fixation, less pollution by pesticides and fertilizers	Higher crop yields, economies of intrants
Result: Increased spatio-temporal landscape heterogeneity	Higher species diversity and evenness?	Better habitat conditions, higher diversity		Benefits of ecosystem services?

A.V.1 Expected impacts on weeds

Both the replacement of curative chemical weed control by IWM-techniques (that are often less efficient) and the introduction of agri-environment schemes such as OSFs would have rather positive effects on several weed species (see also Table 5). OSFs may especially benefit late flowering weed species that are normally killed by soil tillage or herbicides after crop harvest (Hilbig, 1997) but see (Marshall *et al.*, 2005; Pekrun and Claupein, 2006). However, weed seed production in stubble fields or rotational set-aside may be limited by mowing operations (Clarke *et al.*, 1993; Dalbies-Dulout and Dore, 2001). Species adapted to annual

crops will thus probably show rather increasing population densities during the phase of annual crops, especially at the end of the phase of annual crops, when the OSFs are introduced (illustrated in Fig. 7). In contrast, the perennial crops may provide rather unfavourable conditions to several arable weed species adapted to annual crops as suggested by several previous studies reviewed in section A.IV.1 above). Therefore, the population densities of such arable weed species may decline during the perennial crops. At the same time, other plant species may profit from the specific conditions in perennial crops including the absence of soil disturbance during several years (see below). Perennial crops may thus cause weed community shifts. Following this hypothesis, the alteration between phases of annual and perennial crops would result in dynamic changes of the weed communities (illustrated in Fig. 7).

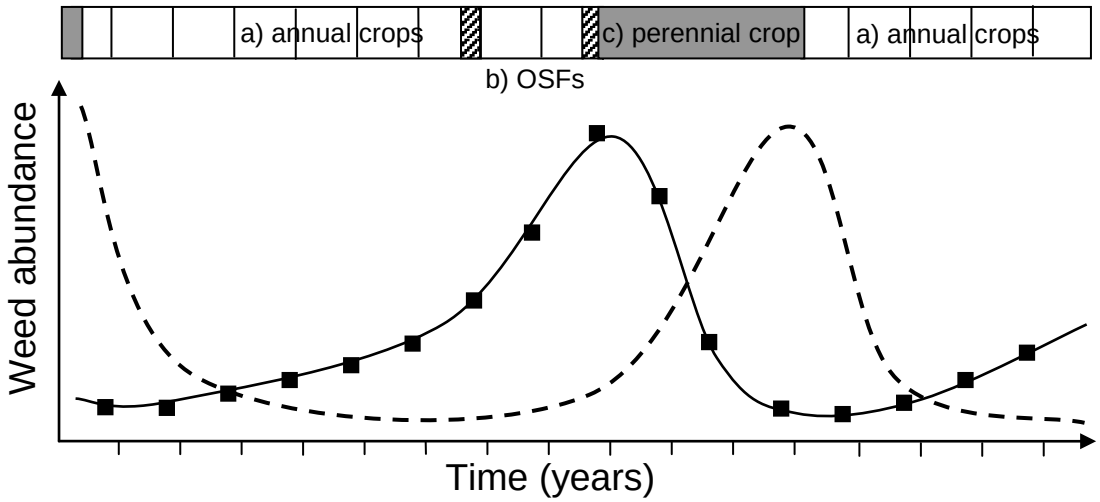

Fig. 7: Illustration of the modified cropping system (upper part) and hypothetical population dynamics of different weed species (lower part).

Upper part: Successions of conventionally managed annual crops (simple crop rotations or monocultures) are replaced by a temporal alteration between periods of (a) annual crops (diverse crop species with integrated weed management and less herbicides) (white boxes), (b) untilled overwinter stubble fields (OSFs) or other agri-environment schemes concerning the whole field area (striped boxes) and (c) perennial crops (PFCs) lasting several years on the field (grey boxes).

Lower part: Hypothetical population dynamics of (i) weed species adapted to annual crops but not to forage crops (black line with dots) and (ii) of species favoured in perennial but not in annual crops (broken line).

This might result in lower pressures of the most noxious arable weeds in the annual crops following the perennial crops. If this is the case, the diversification of crop rotations with

perennial crops might thus be a valuable complement of other IWM techniques, enabling a high yielding crop production and a reduced need for curative weed control including herbicides. In this way, it might contribute to combining high yielding crop production and biodiversity conservation at the dynamic landscape scale. However, it is *e.g.* not clear whether the species favoured by the perennial crops create new weed problems or whether they are quickly suppressed in the following annual crops.

A.V.2 Expected impacts on biodiversity

Different elements of farmland biodiversity will likely profit from the cropping system concept based on the temporal partition of 3 agro-ecological functions. The replacement of herbicides by alternative IWM-techniques may particularly benefit herbicide-sensitive plant species, and thus also organisms feeding or reproducing on the weeds. The introduction of untilled stubble fields as an exemplary 'large-area' agri-environment scheme would improve the habitat quality and food availability for many organisms including birds, mammals, beetles, ants, snails and crickets (Siriwardena et al., 2006). Gillings et al. (2005) showed that the introduction of 10-20 ha overwinter stubbles per 1 km² (1-2% of the area) could reverse the negative population trends of farmland birds in the UK. Finally, the permanent vegetation cover and the lack of soil tillage during several years in the PFCs may provide a rather stable habitat for various organisms that can not survive in annual arable crops, or that need both annual crops and grasslands in close neighbourhood (Summers, 1998; Entz *et al.*, 2002; Buckingham *et al.*, 2006; Henderson *et al.*, 2009). Unlike annual crops, PFCs can provide plant and invertebrate food for higher organisms throughout the year (Tucker, 1992). The biodiversity value of temporary grasslands is probably intermediate between annual crops and permanent grasslands (Thiebaud et al., 2001).

A.V.3 Expected impacts on the environment

All three proposed modifications may also have several, mostly beneficial, effects on the physical environment. The reduction of herbicide use may reduce soil and water pollution and the other drawbacks of herbicides (see section A.II.2). However, some alternative weed control techniques may have negative environmental impacts too. Soil tillage used for weed destruction needs a lot of (fossil) energy and may increase soil erosion and nutrients leaching risks. In contrast, perennial crops and stubble fields are both characterized by temporarily omitted soil tillage, which may thus reduce nutrient leaching and soil erosion compared to

annual crops while increasing organic matter and carbon sequestration in the soil (Sebillotte, 1980; Viaux *et al.*, 1999; Eltun *et al.*, 2002; Entz *et al.*, 2002). Moreover, nitrogen fixing legume species included in the PFC mixtures may reduce the need nitrogen fertilisation in the grassland and in the following annual crops improving the energy efficiency of the system (Entz *et al.*, 2002). However, the organic matter and nutrients accumulated during the period of the perennial crop may only partly be used by the following annual crops, while other parts may be lost through leaching, especially if the temporary grassland is terminated by deep ploughing (Viaux et al., 1999).

A.V.4 Expected impacts on crop production

Introducing perennial crops into crop rotations may have various (positive and negative) impacts on crop yields and farm profitability. The economic profitability of perennial crops may be lower than for annual (cash) crops due to lower marked prices. The low economical value of forage biomass might however be partly compensated for by rather low production costs (Bulson *et al.*, 1996; Entz *et al.*, 2002). Moreover, perennial crops create other long-term amenities, including improvements of soil structure and fertility and reductions in pest pressures (Entz *et al.*, 2002; Katsvairo *et al.*, 2006a). Therefore, perennial crops may also lead to significant yield increases and savings of fertilizer and pesticide inputs in the subsequent annual crops. In addition to these variations, public subsidies may favour or penalize perennial crops. In Iowa, USA, perennial alfalfa get *lower* subsidies than annual crops such as corn and soy bean (Liebman *et al.*, 2008). In the European Union, all crop types should get the same amount of subsidies ('decoupling') since the application of the 2003 CAP reform (which may differ in the member states). In some European countries or regions, mixed farming systems may even *profit* from specific subsidies in the framework of the 'second pillar' of the CAP.

The importance of the different impacts on crop yields and farm profitability will depend on climatic, agronomic, economic and politic factors and may thus strongly differ between regions and farming systems. The three studies cited in the following have thus only an exemplary character.

- A Canadian study suggests that production cost of forage-based systems was lower than for continuous grain production systems but higher than a wheat-fallow system. Interestingly, including a 2- or 3-year forage crop in a 6-year rotation was found to

significantly reduce the variability of the farmers' income, which may be more important than the absolute amount of income (Zentner cited in Entz *et al.*, 2002).

- In a study of Olesen *et al.* (2002) in Denmark, the yield benefits caused by the inclusion of a grass-clover ley could not fully compensate for the yield reduction as a result of leaving 25 % of the rotation out of cash crop (cereal) production.

- In a study of Liebman *et al.*, (2008), the economic profitability of the farming system could be improved by including alfalfa crops into corn–soybean rotations, but the government subsidies reduced this advantage from 7 % to 1 %.

The need for (and therefore the prices of) herbal forages decreased during the last decades due to the separation of crop and livestock production and the shift towards grain forage such as maize. In the future, the demand and profitability of perennial crops might however increase again as these kind of crops are increasingly used to produce energy or raw materials for different industries. Tilman *et al.*, (2006) suggested that 'Low-Input High-Diversity' grasslands may produce biomass (*e.g.* for bio-fuels) with a negative carbon balance and higher yields compared to different monocultures.

A.VI THE RESEARCH PROJECT

A.VI.1 Objectives and questions

The diversified cropping system proposed in section A.V should alleviate the 'weeds trade-off' and contribute towards a more sustainable agriculture. This system relies on the 'weed regulation function' of PFCs. It is thus most essential to study the impacts of perennial crops on weeds and to test the hypothesis of weed community shifts away from species that are most noxious in annual crops. It is also necessary to improve the understanding of the underlying mechanisms (Table 4). This is essential to predict the impacts on weed populations and community dynamics and to successfully use this hypothetical 'ecosystem service' provided by perennial crops. The following research questions will therefore be addressed in this thesis:

- How do weed populations and communities react to PFCs?

- Which species are suppressed, which are favoured in and after PFCs? Do perennial crops reduce the problem of some weed species and create others?
- Do weed species with similar biological response traits (functional groups) react in similar ways?
- What are the most important mechanisms behind the impacts?
- What grassland management options are most appropriate?

A.VI.2 Structure of the thesis

This thesis analyzing the impacts of PFCs on weeds comprises a literature review that is included in the General Introduction (section A.IV.1) and four empirical chapters (C.I - C.IV) corresponding to four research approaches, that are organized on a hierarchical scale (illustrated in Fig. 8).

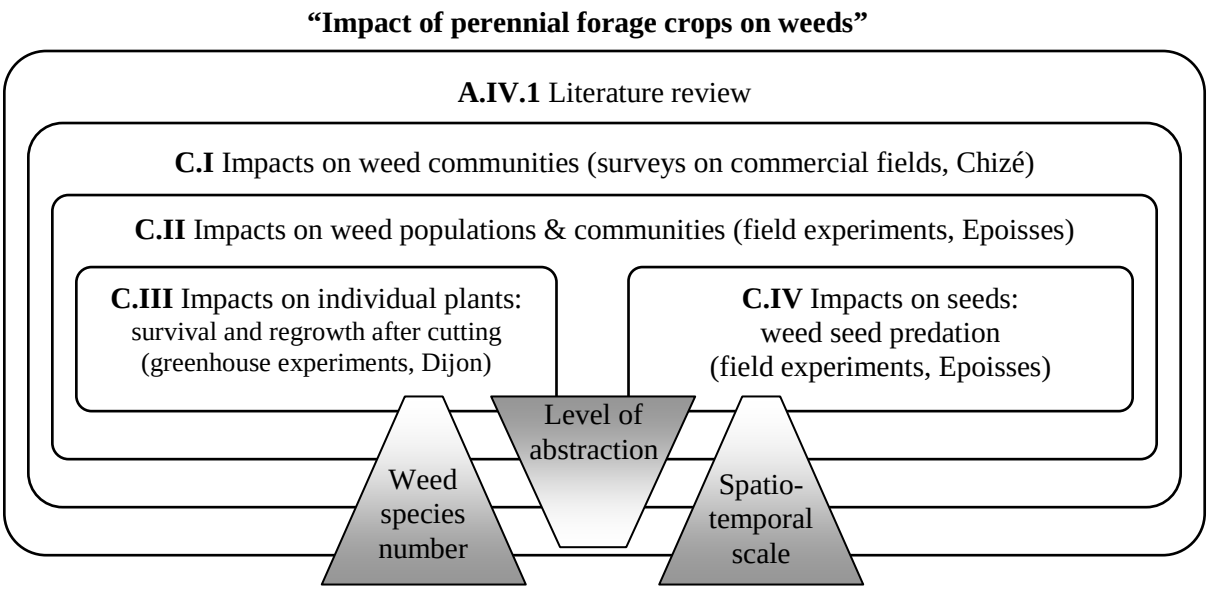

Fig. 8: Structure of the research project showing 4 empirical approaches.

The first empirical chapter C.I deals with the impacts of crop rotations including PFCs on weed communities. It is based on weed surveys over a large number of commercial fields in

the ‘Chizé’ region in Western France, that were realized in collaboration with other scientists and students within the framework of the ‘ECOGER’ research project running from 2006 to 2009 (see ‘Context and Funding’ at the beginning).

The second research approach (C.II) is based on a field experiment designed to compare weed population dynamics between annual and perennial crops with different management options on smaller temporal and spatial scales and with higher temporal and spatial resolutions. The experiment was conducted from 2006 to 2009 on the INRA experimental farm in Dijon-Epoisses. It allows also analyzing several of the hypothetical underlying mechanisms (*c.f.*, section A.IV.2).

Two of these hypothetical mechanisms will also be analyzed in more detail in the two last chapters. Chapter C.III addresses the impacts of cutting on the survival and regrowth capacities of individual weed plants after cuttings, thus a probably important mechanism for the impact of PFCs on weeds that is not frequently studied. It is based on different greenhouse experiments realized in 2007 and 2008 in Dijon. Chapter C.IV deals with the impact of seed predation on weed population dynamics in perennial forage crops. It is based on a short literature review and data from field experiments realized in 2007 and 2008. These two mechanisms are less well known than other mechanisms linked to soil tillage and competition, which are more important and therefore better studied in annual crops.

The following part B will give an short overview of the different methods used for these four research approaches. Part C contains the results, presented as scientific articles or manuscripts. A final part D (general discussion) compares the different findings of the four empirical chapters and discusses general implications, advantages and shortcomings of the different methods and possible applications.

B OVERWIEW OF THE MATERIALS & METHODS

B.I ANALYZING THE IMPACTS OF TEMPORARY GRASSLANDS ON WEED COMMUNITIES: LARGE-SCALE FIELD SURVEYS

B.I.1 Rationale

The objective of this study was to analyze the impacts of arable crop rotation including PFCs on weed communities. The analysis was done in **two steps**.

The **first step** (corresponding to Article 1) consisted in a simple comparison of the weed communities in 7 different current crops comprising alfalfa (*Medicago sativa*)-based forage crops, the most frequent perennial crop, and six annual crops chosen among the most frequent crops in the study region (Fig. 9). Differences in weed communities between perennial and annual crops were analysed and compared to the overall weed community variability in the region dominated by annual crops. Hypothetical differences in the species composition would be a first indication that annual and perennial crops could promote different weed species.

The **second step** (corresponding to Article 2) consisted in an analysis of the weed community trajectories during crop rotations including PFCs using a space-for-time-substitution design. The weed species composition, richness and frequency of functional groups were compared between four groups of fields representing four stages of a crop rotation: a) winter wheat fields following several years of annual crops, b) first-year alfalfa fields following annual crops, c) older alfalfa fields, and d) winter wheat fields following perennial alfalfa (see Article 2 for details). The second analyse was thus limited to the most frequent annual crop (winter wheat) and the most frequent perennial crop (alfalfa) of the Chizé region. It included the crop sequence histories of each field permitting to analyze long-term effects of PFCs and to obtain information on weed community trajectories during crop rotations including annual and perennial crops.

B.I.2 Methods in analyzing weed composition and crop rotation histories

These two analyses were based on weed surveys in the '*Chizé*' research area (*zone atelier 'Plaine et Val de Sèvre'*), comprising about 18000 fields and 450 km², situated in the Niort plain in Poitou-Charentes, western France (Fig. 9). Weed surveys were realized in 2006, 2007,

and 2008 within the framework of the collaborative research project '*Gestion durable des ressources naturelles en plaine céréalière: le rôle central des surfaces pérennes dans les agro-écosystèmes céréaliers'* involving different INRA and CNRS research teams that were part of the ECOGER project (see the 'Context and funding' section for details). Weed surveys were mainly realized by members of the 'weed biology and management' research group (UMR BGA, INRA Dijon) and of the 'Agronomy' research group (UMR '*Agronomie*', AgroParisTech).

The taxonomy of plant species followed Tela-Botanica (http://www.tela-botanica.org/page:eflore). Weed species composition in each field was based on species frequencies on the field scale which were calculated by presence-absence data from 30-32 plots surveyed per field (see Methods of Articles 1 and 2 for further details on the weed surveys). Crop volunteers were excluded from all analysis, even though they are often also considered as weeds (the term 'weed' is defined in Annexe 2). Crop volunteers are often closely associated to the preceding crops and may thus obviously increase the differences in the weed species composition.

While the first analysis needed only information on the current crops, analysis 2 was based on the crop sequence history of each field which was taken from a databank of the common ECOGER-research project containing the land-use data of the whole study area. This huge dataset was established by annually recording the crop species grown on each of the 18000 fields (with varying geometry) since 1995 and mapping it into a GIS databank (see Lazrak *et al.*, 2009 for details).

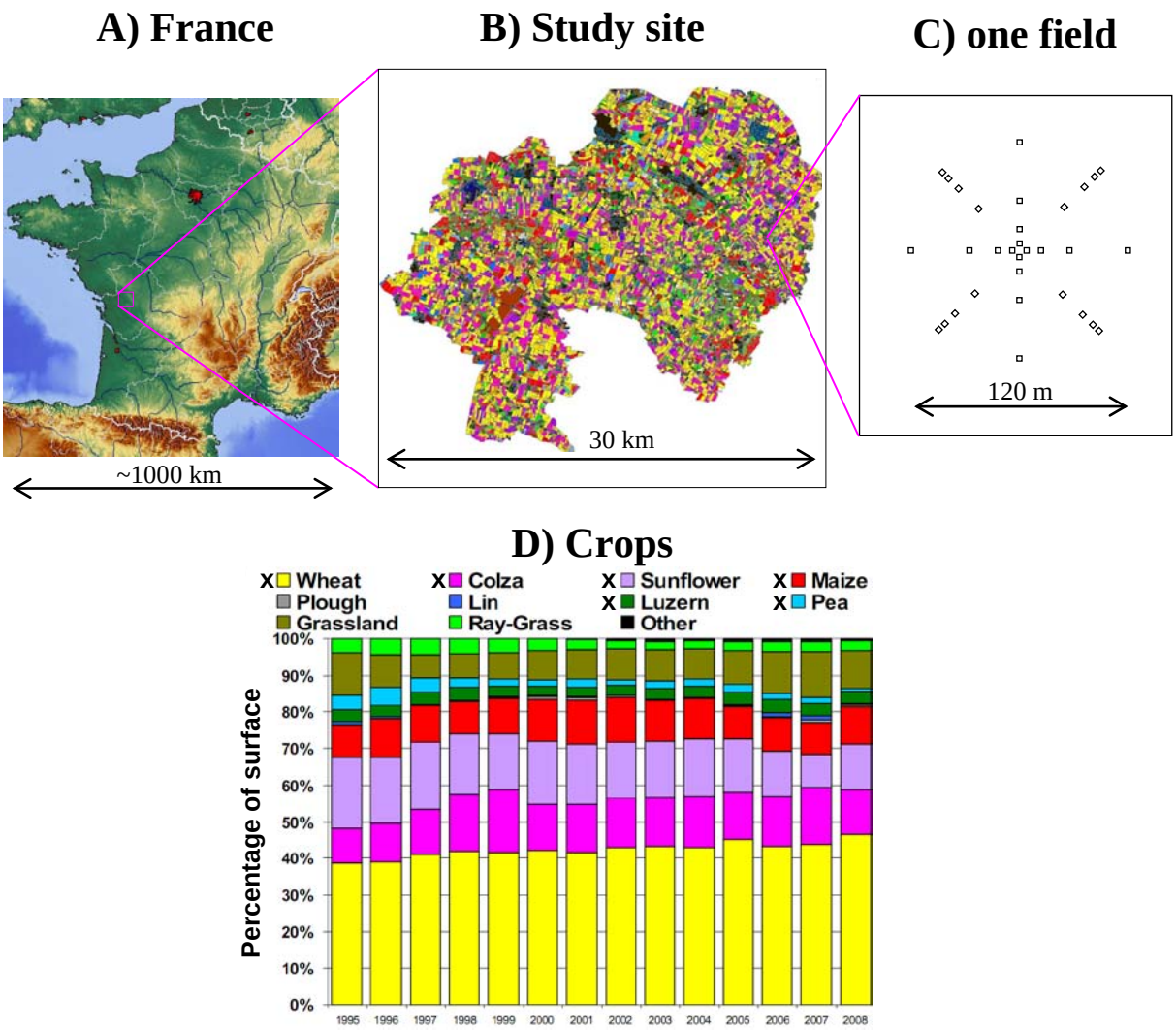

Fig. 9: **A**) Geographic position of the study region in Western France, **B**) map of crops grown at the study site in 2008, **C**) the 'star' configuration of the 32 vegetation *relevés* in each field centre, **D**) temporal development of the principal crops on the study region from 1995 to 2008.

Figures B and D are reproduced from a slideshow presented by Vincent Bretagnolle at the final ECOGER meeting 24-25 March 2009[18]

B.I.3 Statistical analysis

For each analysis, the numbers of fields in the different field categories were set according to the frequencies in the study area. Only the group of wheat fields following perennial alfalfa was increased to improve statistical power (see Table 1 in Article 2). For both analyses, weed

[18] available at http://www.inra.fr/content/download/15865/269357/version/1/file/bretagnolle.pdf and at http://www.inra.fr/audiovisuel/web_tv/colloques/ecoger/bretagnolle.

species composition was compared using Canonical Discriminant Analysis (CDA, Kenkel et al., 2002). Afterwards, global and pairwise differences of species communities between groups of fields were statistically tested using Analysis of Similarities (ANOSIM, Clarke, 1993), a robust non-parametric method adapted to multivariate data with many 'zeros' and not necessarily following multivariate normal distributions. Indicator Species Analysis (ISA, Dufrene and Legendre, 1997) was used to identify the weed species with the most contrasting differences in presences and frequencies.

Functional groups (FG) were defined according to the species taxonomy (opposing grasses and broad-leaved species), life cycle (opposing annual, intermediate and perennials species) and morphology of broad-leaved annual species (opposing upright, creeping, rosette and other species, see Article 2 for further details on FG definition and Annexe 3 for species repartition to the eight FGs). While a lot of rare species had to be excluded from the multivariate analysis, all species could be included in the analysis of functional groups (see Articles 1 and 2 for details on the methods).

B.II FIELD EXPERIMENTS ANALYZING THE IMPACTS OF TEMPORARY GRASSLANDS ON WEED POPULATIONS (EPOISSES)

B.II.1 Rationale

Previously published experimental results and large-scale weed surveys suggest strong impacts of PFCs on weed population dynamics and community composition. However, the impacts of PFC management options and the underlying mechanisms are not well understood. This would also be necessary to construct predictive models. Therefore, a field experiment was conducted to better understand the impacts of PFCs on different annual arable weeds. In contrast to previous experiments, comparisons between annual and perennial crop treatments are not confounded with differences in herbicide treatments.

B.II.2 Design of the field experiment

The field experiment was based on a comparison of 9 crop treatments with 4 replicate plots (75m² each) distributed on the field of an experimental farm. Six crop treatments represented

perennial crops with different management options (crop species, sowing date and cutting frequency), and three treatments represented a succession of annual crops varying only by the intercrop management (see Table 6 in Manuscript 3 for details). The natural soil seed bank of the experimental field was supplemented by homogeneously adding seeds of 17 common annual weed species (see Table 7 for species names) on all experimental plots. One sixth of each plot stayed unsown for control (see methods in Manuscript 3 for details).

B.II.3 Data collection

The development of weed populations and community dynamics was investigated by determining and counting the number of plants of all species every 4-7 weeks in spring, summer and autumn on permanently installed quadrats in the sown and unsown zones. Additionally, the aboveground biomass of crops and all weed species was measured 5-6 times per year to assess the competitive relations between the species.

B.II.4 Statistical analysis

The temporal development of weed species composition in the nine crop treatments was compared using Multiple Response Permutation Procedure (MRPP, McCune and Grace, 2002) with pairwise tests at each measurement date. Indicator Species Analysis (ISA, Dufrene and Legendre, 1997) was used to calculate and test 'Indicator Values' (IV) for the emerged weed plants at the end of the experiment.

B.III GREENHOUSE EXPERIMENTS ANALYZING THE REGROWTH CAPACITY OF WEED PLANTS AFTER CUTTING

B.III.1 Rationale

PFCs are harvested several times per year which is one of the most important differences to most annual crops. Forage mowing creates frequent disturbances of the aboveground vegetation, destroying the upper parts of the shoots of both the forage and the weed plants. In PFCs, weed population and community dynamics may thus strongly depend on the plant's capacity to survive, grow and reproduce after such cutting operations. There are several other situations, where weeds may be submitted to repeated physical disturbances of the aboveground plant organs, including mowing in set-aside fields (Dalbies-Dulout and Dore,

2001), field margin strips (De Cauwer *et al.*, 2005), permanent grasslands (Magda *et al.*, 2003), in-row mowing for weed control in annual row crops (Donald, 2000; , 2007) or vineyards and mowing of cereal crops at harvest. Weed shoots may also be destroyed by grazing, which is sometimes specifically used for weed control (Gill and Holmes, 1997), but grazing is generally less homogeneous concerning the height, space and time of the disturbance than mowing. Despite this variety of situations, the regrowth capacity of weed plants has rarely been studied and the factors determining plant survival, growth and reproduction after cutting are not well known.

B.III.2 Design of the greenhouse experiments

From the list of hypothetical variables (see introduction and Tab. 1 of Article 4), the impacts of (1) *weed species*, (2) *plant size*, (3) *plant age*, (4) *cutting height*, and (5) *interactions between cutting and competition* on the regrowth ability of weed (and crop) plants were investigated by specific experiments conducted in 2007 (Article 4) and 2008 (Article 5 and Bonnot, 2008, master I thesis co-supervised by the present author).

B.III.2.1 Differences between species

In 2007, the regrowth capacity was compared between 10 plants species (containing grasses and broadleaved species, annual and perennial species, crops and weeds, see Article 4 for details). In 2008, 16 species representing the same functional groups were compared in the same way (Bonnot, 2008).

B.III.2.2 Plant biomass

The impact of plant biomass before cutting was assessed for 10 species in 2007 (Article 4) and for 4 species in 2008. To increase the intraspecific variability in plant biomass before cutting, parts of the plants were placed in partial shadow (Article 4).

B.III.2.3 Plant age

The effect of plant age was tested for 2 species in 2007 and for 4 species in 2008. In 2007, plants sown at three dates (differing by 3 weeks each) were cut at the same date (Article 4). In 2008, plants sown at the same date were cut at 4 dates (differing by 4 weeks) (Bonnot, 2008).

B.III.2.4 Cutting height

In 2008, the effect of cutting height was tested for four species (containing crops and weeds, grasses and broadleaved species). Seven treatments were compared varying by the cutting height and the quantity of leaves and buds remaining after cutting (Bonnot, 2008).

B.III.2.5 Interactions between cutting and competition

In 2008, interactions between cutting and competition were analyzed for plants of 12 weed species grown in small experimental plant communities. Cutting and competition treatments were crossed using a 2x2 factorial design where the potential interactions could be analyzed (Article 5).

B.III.3 Cutting treatment and data collection

In all experiments except the tests of cutting height, plants were manually cut at a standardized height (about 5 cm above soil surface) using a pair of scissors. As a control, 4 supplementary plants of each species were left uncut to compare their productivity with the cumulated productivity of cut plants (see details in Article 4). In some experiments, the cutting treatments were repeated several times, *i.e.* regrown shoots were repeatedly cut at the same height to analyze long-term effects. For each species and experimental modality, at least 4 replicate plants were used, in some experiments up to 12.

Weed regrowth was characterized by measuring the aboveground biomass production until the next cutting. Moreover, non-destructive measurements of the plant height and the leaf area were used in some experiments to record regrowth dynamics between the cuttings. The leaf area was determined by image analysis of plant photos in collaboration with two master students co-supervised by the present author, Frederic Henriot (2007), and Rémi Bonnot (2008), see also Article 4 for details.

B.IV FIELD EXPERIMENTS ANALYZING WEED SEED PREDATION

B.IV.1 Rationale

Unlike most annual crops, PFCs are characterized by the complete absence of soil tillage as well as permanent vegetation during several years. Both characteristics may have various

impacts on several phases of the weed life cycle (see general introduction). One rather unknown mechanism is weed seed predation, *i.e.* the consumption of weed seeds by animals. Weed seed predation has very recently gained much interest in agronomic and ecological research. It may have very strong impacts on weed population dynamics making it interesting for Integrated Weed Management (Westerman *et al.*, 2005). On the other hand, favouring weed seed predation may be favourable to seed eating organisms and enhance farmland biodiversity at several trophic levels.

In PFCs, weed seed predation might be favoured by three mechanisms. i) The absence of soil tillage prevents weed seeds to be buried in the soil. Thus all newly produced weed seeds stay on the soil surface where they are more accessible to seed predators. ii) Reduced applications of pesticides in PFCs compared to annual crops may be favourable to predatory organisms. iii) The permanent vegetation cover as well as the absence of soil tillage create a more stable habitat that may be preferred by seed eating animals over annual crops. Weed seed predation might thus cause parts of the differences in weed communities between annual and perennial crops observed in the weed surveys in the Chizé region, the field experiment and in previously published studies. Several experimental studies were conducted to investigate (1) whether seed predation rates differ between common annual weed species and (2) to analyse the impact of vegetation cover.

B.IV.2 Measuring weed seed predation

Weed seed predation was measured using ‘seed cards’ (Westerman *et al.*, 2003a) consisting by seeds slightly glued to sandpaper strips that were fixed on the soil surface with nails. Two types of negative controls were used: (A) Seed cards were put into total exclusion cages (boxes made from metal wire gauze with 1 mm × 1 mm mesh size) permeable to wind and rain excluding any type of seed predator. (B) Presenting plastic beads instead of weed seeds. Moreover, vertebrate exclusion cages (boxes made from metal fence wire with 12 mm × 12 mm mesh size) were used in the 2008 experiment to separate predation by vertebrates and invertebrates (see Article 8).

B.IV.3 Design of the seed predation experiments

B.IV.3.1 Weed species

Differences in seed predation rates between weed species were tested in 2007 in an organic wheat field near Dijon and in 2008 on the different plots of the Epoisses field experiment described in Manuscript 3. In both experiments, seed predation rates were compared for seven common annual weed species, chosen from the 17 weed species sown in the Epoisses field experiment (compare Table 2 of Article 6 and Table 7 of Manuscript 3).

B.IV.3.2 Vegetation cover

The impact of vegetation cover on weed seed predation was tested in 5+ crop treatments of the field experiment described in Manuscript 3. These crop treatments were chosen (i) to represent a wide gradient of vegetation cover from bare soil to uncut perennial crops, (ii) to find out whether the *quality* of the vegetation (grass *vs.* legume crop) or the vegetation *quantity* (cut *vs.* uncut plots) is more important for seed predation rates. The experiments were repeated at three different periods (April, Mai and July 2008). Three weed species were tested at all periods, seven species at one period (July). In the July trial, two additional treatments were included: mown and unmown field margin strips, that were located on the same experimental farm in Epoisses close to the experimental field (Article 7). For each period, weed species, crop treatment and exclusion treatment, 4 spatial repetitions were used.

C RESULTS (Articles & Manuscripts)

C.I IMPACTS OF TEMPORARY GRASSLANDS ON WEED COMMUNITIES (CHIZÉ)

C.I.1 **Article 1:**

Meiss, H., Médiène, S., Waldhardt, R., Caneill, J. & Munier-Jolain, N. (2010a)

Contrasting weed species composition in perennial alfalfas and six annual crops: implications for integrated weed management.

Agron. Sustain. Dev. **30**, 657-666.

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Research article

Contrasting weed species composition in perennial alfalfas and six annual crops: implications for integrated weed management

Helmut MEISS[1,2], Safia MÉDIÈNE[3], Rainer WALDHARDT[2], Jacques CANEILL[1], Nicolas MUNIER-JOLAIN[1]*

[1] Institut National de la Recherche Agronomique (INRA), UMR 1210 Biologie et Gestion des Adventices, INRA / ENESAD / Université de Bourgogne, 17 rue Sully, BP 86510, 21065 Dijon Cedex, France
[2] Institute of Landscape Ecology and Resources Management, Division of Landscape Ecology and Landscape Planning, Justus-Liebig-University Giessen, IFZ, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany
[3] AgroParisTech, UMR 211 INRA-AgroParisTech, BP 01, 78850 Thiverval-Grignon, France

(Accepted 9 October 2009)

Abstract – Weed communities are most strongly affected by the characteristics and management of the current crop. Crop rotation may thus be used to prevent the repeated selection of particular weed species. While weed communities are frequently compared among annual crops, little is known about the differences between annual and perennial crops that may be included in the rotations. Moreover, nearly all existing studies (17 articles reviewed) are based on local field experiments rather than commercial fields. We compared the weed composition in perennial alfalfas (*Medicago sativa*) and six annual crops: winter wheat (*Triticum aestivum*), oilseed rape (*Brassica napus*), pea (*Pisum sativum*), sunflower (*Helianthus annuus*), maize (*Zea mays*) and sorghum (*Sorghum bicolor*) using data from 632 commercial fields in western France. Weed species composition showed the strongest dissimilarities between perennial alfalfas and all annual crops, followed by the well-known differences between autumn- and spring/summer-sown annual crops. Indicator Species Analysis showed that most weed species either preferred perennial alfalfas (including *Taraxacum officinale*, *Veronica persica*, *Crepis* spp., *Poa trivialis*, *Silene latifolia*, *Capsella bursa-pastoris* and *Picris* spp.) or annual crops (including *Mercurialis annua*, *Galium aparine*, *Fallopia convolvulus*, *Chenopodium album* and *Cirsium arvense*). Perennial alfalfas thus suppressed many weeds that are widespread (and sometimes problematic) in annual crops while favouring other species. Shifted weed composition and reduced frequency of several noxious weeds suggest that perennial alfalfas may be used as a valuable part of integrated weed management, reducing the need for herbicides and sustaining plant and animal diversity in agricultural landscapes.

crop diversification / temporary grassland / perennial forage crop / alfalfa / *Medicago sativa* / plant community composition

1. INTRODUCTION

Weed communities in arable fields are mainly characterised by the current crop type and associated farming practices (Doucet et al., 1999). These anthropogenic factors are probably more important than environmental factors linked to, e.g., soil type and climate (Fried et al., 2008). Each crop and associated management practices provide more or less specific conditions that act as filters (sensu Belyea and Lancaster, 1999) offering different ecological niches for weeds. Rotating dissimilar crops constitutes an important part of preventative weed management (Liebman and Dyck, 1993; Bellinder et al., 2004; Nazarko et al., 2005; Smith and Gross, 2007). It may avoid selection for, and rapid population increases in, particular weed species adapted to one crop type, such as may happen when one crop is cultivated during consecutive years ('monoculture').

Doucet et al. (1999) tried to disentangle the effects of intrinsic crop characteristics and crop management practices on weeds. They concluded that management had stronger influences than crop characteristics; however, both are often closely associated. First, the crop type influences several management practices important for weeds including the sowing season, the usable types of (selective) herbicides, the possibilities of mechanical weed control in the crop, and the harvesting date (determining, e.g., the potential for weed seed production). Second, several management practices (e.g., sowing date and density, fertilisation, irrigation, pest control) affect crop growth dynamics and thus crop-weed competition.

The 'weed-regulating function' of crop rotations may, however, be restricted if crop types and management practices are too similar or if the rotations are too short. To avoid this

* Corresponding author: munierj@dijon.inra.fr

situation, crop rotations should be diversified. One possibility may be the introduction of *perennial* crops such as alfalfa/lucerne (*Medicago sativa*), clovers (*Trifolium* spp.), other legumes (Fabaceae), grasses (e.g. *Dactylis glomerata*, *Festuca* spp., *Lolium* spp., *Phleum pratense*, *Poa pratensis*) and various legume-grass mixtures (Freyer, 2003). Such crops are also called 'temporary grasslands', 'leys', 'sod crops', 'fodder crops' or 'hay crops'. Such perennial crops stay on the field for several years before being converted to annual crops again. They are mostly used for livestock forage production, but may also be used to produce energy or raw material for industries (Tilman et al., 2006). The amelioration of soil fertility and the regulation of pest and weed infestations are further reasons for interrupting sequences of annual crops with temporary grasslands (Katsvairo et al., 2006). The appearance of cheap fertilisers and pesticides and the separation of crop and livestock production are the main reasons for the decline in temporary grasslands in conventional cropping systems of many regions (Freyer, 2003). Today, temporary grasslands are mainly used in organic or low-input cropping systems. The need for improving the sustainability of cropping systems has recently increased the interest in diversifying farming systems with perennial crops (Katsvairo et al., 2006).

Perennial crops may have strong impacts on the weed composition. Compared with annual crops, perennial forage crops are characterised by (a) reduced soil disturbances due to the absence of soil tillage for the whole duration of the crop (about 2–6 years), (b) increased aboveground disturbances caused by frequent hay cuttings (1–5 times per year) or grazing, (c) high and temporally extended competition caused by permanent and intense canopy closure and deep and dense rooting systems, (d) reduced or omitted herbicide use (Bellinder et al., 2004), and possibly (e) allelopathic compounds released by some perennial crops including alfalfa (Khanh et al., 2005). These characteristics may have various direct and indirect impacts on weeds. Established weed plants may benefit from the absence of soil tillage and from the reduced herbicide use. In contrast, they may suffer from the high competition (Schoofs and Entz, 2000) and from the regular cuttings (Norris and Ayres, 1991; Meiss et al., 2008). Cuttings may temporally reduce the competition for light, but regrowth of forage crops is generally fast (Gosse et al., 1988; Meiss et al., 2008) and belowground competition for nutrients and water remains strong. The absence of soil tillage and the permanent vegetation cover may cause an accumulation of plant litter that may form a weed-suppressive mulch. In perennial crops, soil characteristics (organic matter, humidity, nutrients) and microclimatic conditions (temperature, light quantity and quality) relevant to weeds may be different to annual crops (Entz et al., 2002). Therefore, some weed species may not be able to germinate without soil disturbance (Huarte and Arnold, 2003), and a delayed nitrogen availability in legume-based cropping systems (in contrast to mineral N fertilisation) may favour species with larger seeds over smaller seeds (Liebman and Davis, 2000). Finally, the absence of soil tillage and the permanent vegetation cover may favour weed seed decay or seed predation by animals (Westerman et al., 2005). All these factors may potentially change weed demography and species composition in perennial forage crops. However, differences between annual and perennial crops are poorly documented, in contrast to comparisons between annual crops (Doucet et al., 1999; Murphy et al., 2006; Fried et al., 2008). Available empirical studies analysing the effects of forage crops on weeds are summarised in Table I.

Most of the studies report reduced seed or plant abundance of several noxious weeds at the end of the forage crops or in the following crop. Disadvantaged species include mostly annual dicotyledonous species such as *Abutilon theophrasti*, *Amaranthus* spp., *Brassica kaber* and *Galium aparine*, but also some problematic annual grasses such as *Apera spica-venti* and *Avena fatua*, and a few perennial weeds such as *Cirsium arvense*. Meanwhile, several studies indicate that other species may profit from the forage crops including perennial broad-leaved weeds such as *Taraxacum officinale* and *Rumex* spp., some annual broad-leaved species such as *Thlaspi arvense* and some grasses such as *Elymus repens* and *Poa* spp. (see references in Tab. I). For several weed species, different studies report variable or even contradictory results (Tab. I).

Most available studies were based on local field experiments, whereas only one study was conducted on a larger number of fields from commercial farms (Ominski et al., 1999). Moreover, many studies refer to forage crops lasting only 1 year (Tab. I), but impacts on weeds may differ in pluri-annual forage crops. Ten out of the 17 available studies concerned North America (Tab. I) but agronomic practices and environmental conditions may be different elsewhere.

The aim of this study was to compare the weed species composition in perennial and annual crops. The current crop is known to have a strong impact on the expressed weed composition. Effects of preceding crops, which have probably the second most important influence on weed communities (Fried et al., 2008), will be studied elsewhere. We used data from >600 commercial fields in western France including the most frequent perennial crop, alfalfa/alfalfa (*Medicago sativa*), and six annual crops: winter wheat (*Triticum aestivum*), oilseed rape (*Brassica napus*), pea (*Pisum sativum*), sunflower (*Helianthus annuus*), maize (*Zea mays*) and sorghum (*Sorghum bicolor*). This study might provide additional knowledge about the potential of perennial crops to contribute to a more sustainable weed management in cereal-based cropping systems.

2. MATERIALS AND METHODS

2.1. Data sampling

The field surveys were conducted in a region of intensive agriculture in western France (46°11'N, 0°28'W). Annual mean precipitation is 779 mm and mean temperature 12.3 °C (5.6 in winter, 18.9 in summer). The commercial fields were part of a large study area (400 km^2, >18 000 fields) supporting research on agriculture and biodiversity since 1994. Weeds were observed in spring and early summer of the years 2006, 2007 and 2008. We compared seven major crop species (see Tab. II for crop names and survey dates). The number of analysed fields per crop roughly corresponded to the relative

Table I. Overview of studies investigating the impacts of temporary grasslands (also termed 'hay crops', 'forage crops', 'sod crops', 'leys') on weeds.

Reference	Type of study[1] (total duration)	Location	Crops or rotations compared[2] (forage crop durations)	Main findings	Species suppressed	Species favoured
Norris and Ayres, 1991	FE (3y)	California, USA	**Alfalfa (?)**, cutting frequency: 25, 31 or 37 days	Foxtail invasion decreased with increasing cutting interval	*Setaria glauca*	
Entz et al., 1995	Interview of 253 farmers	Manitoba, Canada	annual crops after **perennial forages (~3–7y)**	"Weed control benefits" reported by 83% of farmers, lasting for 1y, 2y, or more after forages (11%, 50% and 33% of respondents), higher crop yields		
Andersson and Milberg, 1996, 1998	FE (26y)	Southern Sweden	6y rotations with (i) **grass ley (2y)** (ii) **legume-grass ley (2y),** (iii) spring wheat + fallow	Strong community differences between ley and all annual crops, but not between 3 rotations, no weed problems (herbicides used in cereals only)	Many annual weeds	*T. officinale, Cerastium fontanum, Poa annua*
Gill and Holmes, 1997	Review of FE	Southern Australia	**mown** or **grazed pastures (2–3y)** included in cereal rotations	Grazing or cutting for hay or green manure help control weeds including herbicide-resistant *Lolium sp*. Lower weed seed production	*Lolium* spp., *Avena fatua,*	
Clay and Aguilar, 1998	FE (3y)	South Dakota, USA	corn after (i) corn, (ii) **alfalfa (2y)**	Decreasing weed biomass during forage phase and in corn after alfalfa, same seed bank density but higher % of grasses, higher corn yield, variable seed density & emergence depending on input level	Broad-leaved species, some grasses	Some other grasses
Ominski et al., 1999	Surveys in 117 commercial fields (2y)	Manitoba, Canada	cereals after (i) **alfalfa-grasses (?)** (ii) cereals	Reduced overall weed densities, weed community shifts	*Avena fatua, Cirsium arvense, Brassica kaber, Galium aparine*	*Taraxacum officinale, Thlaspi arvense*
Schoofs and Entz, 2000	FE (2y)	Manitoba, Canada	peas after (i) **forages (1y)**, (ii) wheat	Herbicide-free forages suppressed grass weeds as effective as sprayed wheat, variable effect on broad-leaved weeds (not enough competition), higher pea yields after forages but some herbicides necessary in peas	*Avena fatua, Setaria viridis*	
Sjursen, 2001	FE (8y)	Fryden-haug, Norway	6-y rot. including (i) **grass-clover ley (3y),** (ii) annual crops (with undersowing)	Same seed bank diversity but lower established diversity	Annual broad-leaved	Perennial broad-leaved

Table I. Continued.

Reference	Type of [1] study (total duration)	Location	Crops or rotations compared[2] (forage crop durations)	Main findings	Species suppressed	Species favoured
Cardina et al. 2002; Sosnoskie et al., 2006	FE (35y)	Ohio, USA	(i) continuous corn CCC, (ii) corn-soybean CS, (iii) corn-oats-**hay (1y)** COH (fewer herbicides)	Seed bank composition differed between 3 rotations, rotations more than tillage systems, but rotation*tillage interactions, higher species diversity and evenness in COH. Seed bank diversity influenced by crop diversity. Highest seed bank density in no-till CCC	*Chenopodium album, Setaria faberi*	*Digitaria sanguinalis, Setaria glauca, Stellaria media, C. bursa-patoris, Polygonum pensilvanicum, Veronica arvensis, Oxalis stricta, …*
Bellinder et al., 2004	FE (2y)	New York, USA	2y rot.: **alfalfa (1y)**, **clover (1y)**, rye cover crop, corn	Seed densities increased after rye, similar in alfalfa, clover and corn (despite absence of herbicides and tillage in clover and alfalfa). Alfalfa and clover reduced seed return more than rye. Combined effects of competition and cutting reduced weed growth	*Ambrosia artemisiifolia*	*Chenopodium album, Stellaria media*
Teasdale et al., 2004; Cavigelli et al., 2008	FE (4–10y)	Maryland, USA	(i) 2y conv. corn-soybean, (ii) 3y org. c-s-wheat fallow, (iii) 4+y org. c-s-w **-clover-*Dactylis* hay (1–3y),**	Decreasing weed abund., incr. N availability with rotation length in org. systems. Lower seed banks of broad-leaved species, higher or equal grasses after hay and after wheat. Importance crop starting the rotation (should be weed-suppressive hay). Correlation seed bank – plant densities (R^2 0.01–0.76)	*Amaranthus hybridus, Chenopodium album*	grasses
Albrecht, 2005	FE (8y)	Bavaria, Germany	7y org. rot. including **grass-clover mix (1y)** and **undersown grass- clover mix (1y)**	Grass-clover mix reduced seed bank by 39%; winter cereals, sunflowers, lupins increased seed by 30–40%; potatoes, sown fallow: no change	*Anthemis arvensis, A. spica-venti, C. bursa-pastoris, G. aparine, Lapsana communis, Matricaria recutita, S. media, V. arvensis, …*	*T. officinale, Elymus repens*

Table I. Continued.

Reference	Type of [1] study (total duration)	Location	Crops or rotations compared[2] (forage crop durations)	Main findings	Species suppressed	Species favoured
Heggen-Staller and Liebman, 2006	FE (5y)	Iowa, USA	(i) 2–y: maize-soybean, (ii) 3–y: m-s-triticale+ **red clover (1y)**, (iii) 4–y: m-s-triticale +**alfalfa-alfalfa (1.5y)**	Low *A. theophrasti* seedling survival + fecundity in alfalfa, higher seedling survival + fecundity in maize + soybean in 3- and 4–y rot (75% less herbicides), but pops remained stable. *Setaria faberi* increased in 1 study year	*Abutilon theophrasti*	*Setaria faberi*
Hiltbrunner et al., 2008	FE (15y)	Albertswil, Switzerland	6 crops: wheat, maize, barley, potatoes, oilseed rape, **temporary grassland (2y)**	*Taraxacum officinale* and *Rumex obtusifolius* increased in temporary grassland with time and dominated the weed community in the following crop		*Taraxacum officinale*, *Rumex obtusifolius*

[1] FE, field experiment. [2]: Forage crops are in **bold**.

Table II. Crop species surveyed in the three-year study, with sampling effort and survey periods.

Crop species	Type	Sowing season	Freq.[1]	Number of fields surveyed				Survey periods[2]
				2006	2007	2008	Total (%)	min–max
Alfalfa (*Medicago sativa*)	perennial	autumn or spring	4%	69	61	64	194 (31%)	10 April–17 May
Winter wheat (*Triticum aestivum*)	annual	autumn	38%	98	61	78	237 (38%)	16 Feb.–2 May
Oilseed rape (*Brassica napus*)	annual	autumn	13%	40	0	16	56 (9%)	10 Mar.– 31 Mar.
Pea (*Pisum sativum*)	annual	autumn or spring	3%	21	20	1	42 (7%)	26 Mar.–23 May
Sunflower (*Helianthus annuus*)	annual	spring-summer	14%	21	22	3	46 (7%)	22 May–8 July
Maize (*Zea mays*)	annual	spring-summer	9%	21	22	0	43 (7%)	22 May–8 June
Sorghum (*Sorghum bicolor*)	annual	spring-summer	NA	0	14	0	14 (2%)	8 June–29 June
Total				270	200	162	632 (100%)	

[1] Approximate frequency of the crop in the study area.
[2] The earliest and latest survey dates across all study years.

frequency of the crops in the region except for alfalfas, which were over-represented (Tab. II).

Weed surveys in annual crops were done in 32 quadrats of 4 m^2 (2 m^*2 m) per field arranged along eight transects radiating from the centre of the field. In alfalfas, surveys were realised in 30 quadrats of 0.25 m^2 (0.5 m^*0.5 m) which were arranged on 2–3 parallel transects covering the entire field. Field edges were avoided in both cases. Smaller plot sizes were necessary due to the higher crop vegetation density in alfalfas compared with the annual crops. A statistical method was used a posteriori to test whether the two methods captured the same percentage of species present in the fields. For each field, we calculated the ratio of the observed species richness to the expected total species richness, which was estimated by Chao's formula (Colwell and Coddington, 1994) using the 'specpool' function in the 'vegan' package (Oksanen et al., 2009) of R (R Development Core Team, 2008). The results showed that this ratio did not vary significantly between the seven crops ($F_{6,625}$ = 1.48, P = 0.18). The mean ratios were highest in sorghum (84.0%), lowest in wheat (76.0%) and intermediate in alfalfa (77.3%), suggesting that the methods captured a similar amount of information. This was also confirmed by species accumulation curves (sample-based rarefaction curves) (Gotelli and Colwell, 2001) which were calculated for the quadrats on the field scale using the 'specaccum' function of the 'vegan' package of R. The shape of the curves varied (data not shown), especially between fields with higher and lower species richness, but not between the crops,

suggesting that the amount of information captured by both sampling techniques did not differ. Crop volunteers were not included in the analysis. 197 weed taxa were distinguished, including 161 species and 36 groupings of several species belonging to the same genera.

2.2. Statistical analysis

Presence-absence data from the 30–32 quadrats per field were used to calculate species frequency on the field scale. The percentage of occupied quadrats was used as an indicator of species abundance on the field scale. Different multivariate statistics and ordination methods were used to describe and test the differences between the seven crops. Rare weed species (present in less than 12 fields out of 632) were excluded from the multivariate analysis as they may unduly influence the results (Kenkel et al., 2002). As the survey year (2006, 2007, 2008) had no strong influence on the weed communities in this dataset (data not shown), data from all three years were pooled for comparing the crops.

Canonical Discriminate Analysis (CDA, Kenkel et al., 2002), also known as "Canonical Variates Analysis" was used as a constrained ordination method to visualise the community differences between the crops. CDA finds axes that best separate predefined groups (crops) in multivariate space. Analysis of Similarities (ANOSIM, Clarke, 1993) with the Bray-Curtis dissimilarity measure was used for testing the null hypothesis that crops do not differ in their weed composition. This non-parametric method is recommended for analysing multivariate data containing many zeros and does not rely on assumptions about multivariate normality (Kenkel et al., 2002; Sosnoskie et al., 2006). The ANOSIM-R statistic varies between 0 (no differences between crops) and 1 (maximum difference, crops do not share any weed species). After the global tests, pairwise differences between all crops were calculated and Bonferroni-corrected p-values are reported.

Indicator Species Analysis (ISA, Dufrene and Legendre, 1997) was used to identify and test the weed species showing strongest differences among the seven crops. This method combines information on the species frequency in each crop (presence-absence on the field scale) and on the species abundance in each crop (here: percentage of presence on the quadrats of each field). It returns indicator values (IV) for each species in each crop varying between 0 (species absent from all fields of that crop) and 100 (species is present with highest abundance in all fields of the crop, thus 'perfect indication'). These values are tested for statistical significance using a randomisation technique (4999 permutations of the fields' allocations to crops).

3. RESULTS AND DISCUSSION

3.1. Weed communities

Weed communities showed strong non-random differences between the crops (ANOSIM-R = 0.42, $P < 0.0001$).

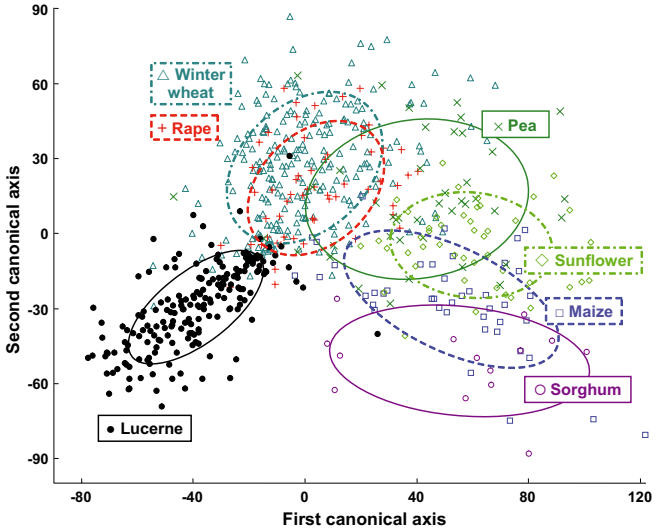

Figure 1. Canonical discriminant analysis (CDA) showing the differences in the weed communities in 7 crops: • alfalfa, △ winter wheat, + oilseed rape, × pea, ◇ sunflower, □ maize, ○ sorghum (each point corresponds to one field, 632 fields in total). 60% confidence ellipses around crop centroids are drawn. Perennial alfalfas had the most distinct weed communities compared with all annual crops. Differences between autumn-sown annual crops (wheat, rape) and spring/summer-sown crops (sunflower, maize, sorghum) were also strong, while peas (sown in autumn or spring) had an intermediate position.

Canonical Discriminant Analysis (CDA) indicated that species composition mainly varied between three groups of crops: (i) perennial alfalfas, (ii) autumn-sown annual crops (wheat, oilseed rape) and (iii) spring/summer-sown annual crops (sunflower, maize, sorghum). Peas, which may be sown in autumn or spring, had an intermediate position between autumn- and spring-sown crops (Fig. 1).

Pairwise comparisons showed that the differences were strongest between alfalfa and sunflower (ANOSIM-R = 0.71, $P < 0.0001$), followed by alfalfa-maize, -pea, -rape, -sorghum and -wheat, while nearly all comparisons between pairs of annual crops were lower (Tab. III). This is consistent with CDA (Fig. 1). Alfalfas had thus the most distinct weed species composition among the seven crops. This difference was even more pronounced than the better–known difference between autumn- and spring/summer-sown annual crops (Tab. III), which is frequently reported in the literature (e.g. Doucet et al., 1999; Murphy et al., 2006; Fried et al., 2008). The originality of our study is the inclusion of perennial crops, which have rarely been documented for commercial fields.

3.2. Indicator species

The strong differences between weed communities in perennial and annual crops were caused both by significant increases in nine species in alfalfas, including *Taraxacum officinale*, *Veronica persica*, *Crepis* spp., *Silene latifolia* and

Table III. Pairwise ANOSIM comparisons of weed communities in 7 crops (Tab. II) sorted by decreasing R-values. Pairwise differences are thus strongest between alfalfas and most annual crops although differences between pairs of annual crops are mostly significant too.

Crops compared			ANOSIM-R
Alfalfa	-	Sunflower	0.71****
Alfalfa	-	Maize	0.71****
Alfalfa	-	Pea	0.61****
Sorghum	-	Rape	0.60****
Alfalfa	-	Rape	0.57****
Sunflower	-	Sorghum	0.56****
Maize	-	Rape	0.56****
Alfalfa	-	Sorghum	0.53****
Alfalfa	-	Wheat	0.53****
Sorghum	-	Wheat	0.50****
Sorghum	-	Pea	0.46****
Sunflower	-	Rape	0.43****
Maize	-	Wheat	0.39****
Pea	-	Rape	0.32****
Sunflower	-	Wheat	0.27****
Sunflower	-	Pea	0.25****
Pea	-	Maize	0.25****
Sunflower	-	Maize	0.18****
Rape	-	Wheat	0.17**
Sorghum	-	Maize	0.16ns
Pea	-	Wheat	0.05ns

****: $P < 0.0001$; **: $P < 0.01$; ns: not significant. P-values are Bonferroni-corrected.

Capsella bursa-pastoris, while about 24 other species appeared mainly in annual crops [see Tab. IV for names and indicator values (IV) of all species in all crops]. Some weed species had relatively high frequency and abundance in several annual crops. For example, *Veronica hederifolia*, *Galium aparine* and *Fallopia convolvulus* were indicator species for wheat, rape and pea, and *Mercurialis annua*, *Convolvulus arvensis* and *Solanum nigrum* for pea, sunflower, maize and sorghum crops (Tab. IV). In contrast, almost no species had high frequency in both annual crops and perennial alfalfas except *Veronica persica* in alfalfa and wheat and *Capsella bursa-pastoris* in alfalfas and sorghum (Tab. IV).

3.3. Differences among annual crops

Among the annual crops, typical weed germination periods may explain large parts of the observed differences between the crops, as documented in previous studies (e.g. Roberts, 1984; Hald, 1999; Fried et al., 2008). Weed communities in rape crops (sown between August and October) were characterised by species preferentially emerging in autumn or late summer including *Euphorbia helioscopia*, *Sinapis arvensis* and *Viola tricolor*. Winter wheat (sown in October–November) was characterised by winter-emerging species such as *Veronica hederifolia*, *Galium aparine* and *Papaver rhoeas*. Peas (sown in November or February–March) were dominated by early spring-emerging species including *Kickxia spuria*, *Polygonum aviculare* and *Fallopia convolvulus*, and sunflower, maize and sorghum crops (sown in April–May) by late spring-emerging species including *Amaranthus retroflexus*, *Setaria* spp., *Solanum nigrum*, *Chenopodium album* and *Polygonum persicaria* (Tab. IV). It should be noted that weed surveys in the spring/summer-sown crops were conducted several weeks later in the year than all other crops (Tab. II), which could have introduced some additional differences. Conversely, the autumn-sown crops and alfalfas were surveyed during the same season.

3.4. Differences between annual and perennial crops

Figure 2 shows that all species with high frequency in annual crops (all 6 annual crops pooled together) are less frequent in perennial alfalfas and vice versa. While all very frequent species showed clear preferences, only a few species had similar mean frequencies in both crop types: *Stellaria media* and *Alopecurus myosuroides* (Fig. 2).

As the previous studies on weeds in perennial forage crops (Tab. I) are mostly descriptive, the following discussion about the mechanisms that may have caused the differences between the weed communities in annual and perennial crops might be somewhat speculative. Parts of the observed differences might be explained by the morphology of the weed plants that would influence the response to cutting. Previous experiments on individual plants suggest that upright broad-leaved weed species are most strongly affected by cutting, which will destroy large parts of the leaves and of the apical meristems and axial buds needed for regrowth (Meiss et al., 2008). On the contrary, meristems (and leaves) of grasses or broad-leaved species with a flat morphology or rosettes would be less affected by cutting and might regrow more easily. The present study suggests that these morphological traits of broad-leaved weeds may actually be important in field conditions, as many of the species disadvantaged by alfalfas have either an upright morphology, including *Mercurialis annua*, *Chenopodium album*, *Fumaria officinalis*, *Sinapis arvensis* and *Cirsium arvense*, or climb up neighbouring plants, such as *Galium aparine*. In contrast, several of the broad-leaved species favoured by alfalfas have rosettes, including *Sonchus asper*, *S. oleraceus*, *Crepis* spp., *Picris* spp., *T. officinalis* and *C. bursa-pastoris*.

Plant life cycle duration might also explain some of the observed differences between annual and perennial crops. On the one hand, alfalfas favoured several *perennial* species, which has been observed previously (Andersson and Milberg, 1996; Teasdale et al., 2004; Albrecht, 2005; Hiltbrunner et al., 2008). Slower-growing biennial or perennial species probably profited from the absence of soil tillage, which may also be the case in no-till cropping systems or in secondary succession (e.g., Zanin et al., 1997; Murphy et al., 2006). Moreover, perennial species are probably more tolerant to competition and to the repeated cuttings than most annual species. Another

Table IV. Indicator species analysis (ISA) of the weed communities in seven crops. Only weed species with $IV_{max} \geqslant 20$ (maximal IV over the different crops) are shown. High indicator values (IV) are shaded in successively darker shades of grey over the three levels: IV ⩾ 10, IV ⩾ 20 and IV ⩾ 30. Alfalfas are associated with nine taxa. Indicator species of annual crops often show high indicator values in several annual crops, but rarely in annual and perennial crops. Alfalfas were thus characterised by a distinct weed community, suppressing many (noxious) weed species typical of different annual crops while favouring other species.

Weed species	Code	Current crop							Crop with highest IV	*P*
		Alfalfa	Wheat	Rape	Pea	Sunflow.	Maize	Sorghum		
		----------IV----------								
Taraxacum officinale	TAROF	**47**	4	0	0	0	0	7	Alfalfa	0.0002
Veronica persica	VERPE	**39**	12	1	3	1	3	6	Alfalfa	0.0002
Crepis sancta +vesicaria +sp.	CVP	**34**	0	3	0	0	0	0	Alfalfa	0.0002
Veronica arvensis +polita	VERAR	**32**	3	0	1	0	0	0	Alfalfa	0.0002
Silene latifolia	MELAL	**25**	2	1	2	1	1	1	Alfalfa	0.0010
Myosotis arvensis +sp.	MYOAR	**22**	4	3	1	0	0	0	Alfalfa	0.0020
Cerastium arvense +glomeratum	CER	**20**	1	0	0	0	0	0	Alfalfa	0.0014
Poa trivialis	POATR	**20**	3	0	1	0	1	3	Alfalfa	0.0026
Capsella bursa pastoris	CAPBP	**22**	1	8	1	0	0	**20**	Alfalfa	0.0026
Papaver rhoeas +argemone +sp.	PAPRH	4	**20**	2	3	0	0	0	Wheat	0.0070
Veronica hederifolia	VERHE	3	**32**	17	19	0	0	0	Wheat	0.0002
Galium aparine	GALAP	2	**20**	11	13	4	0	0	Wheat	0.0080
Viola arvensis +tricolor +sp.	VIOTR	1	14	**23**	14	2	0	0	Rape	0.0022
Sinapis arvensis	SINAR	1	6	**27**	4	9	2	4	Rape	0.0008
Euphorbia helioscopia	EPHHE	0	1	**32**	3	15	3	6	Rape	0.0002
Reseda lutea +sp.	RES	1	0	**25**	1	10	0	1	Rape	0.0004
Fallopia convolvulus	POLCO	1	16	13	**28**	18	6	2	Pea	0.0002
Polygonum aviculare	POLAV	1	11	5	**20**	4	14	14	Pea	0.0140
Kickxia spuria +sp.	KICSP	0	0	0	**40**	1	6	12	Pea	0.0002
Senecio vulgaris +sp.	SENVU	4	6	9	8	**32**	1	3	Sunflower	0.0002
Solanum nigrum +sp.	SOLNI	0	0	0	14	**25**	9	**21**	Sunflower	0.0002
Mercurialis annua	MERAN	0	5	10	16	**24**	19	14	Sunflower	0.0006
Convolvulus arvensis	CONAR	3	3	0	12	**22**	**26**	**22**	Maize	0.0008
Chenopodium album	CHEAL	0	4	1	17	8	11	**36**	Sorghum	0.0002
Setaria viridis +verticillata +sp.	SET	0	0	0	0	2	**20**	**42**	Sorghum	0.0002
Polygonum persicaria	POLPE	0	0	0	2	5	18	**20**	Sorghum	0.0006
Amaranthus retroflexus	AMARE	0	0	0	0	1	6	**58**	Sorghum	0.0002
Verbena officinalis +sp.	VEBOF	3	0	0	0	0	0	**35**	Sorghum	0.0002
Picris echioides	PICEC	11	0	4	0	0	0	**34**	Sorghum	0.0002
Calystegia sepium	CAGSE	0	0	0	0	0	9	**30**	Sorghum	0.0002
Echinochloa crus galli	ECHCG	0	0	0	0	1	8	**28**	Sorghum	0.0002
Plantago major	PLAMA	0	0	0	1	0	1	**26**	Sorghum	0.0002
Cirsium arvense +sp.	CIRAR	2	7	4	5	8	3	**21**	Sorghum	0.0062

mechanism might be seed predation, which may have stronger impacts on populations of annual species than on perennials and which may be particularly strong in untilled perennial crops with permanent vegetation cover (Westerman et al., 2005). While the perennial species found in alfalfas did not appear with high frequency in any annual crop, other perennial species appeared in sorghum crops including *Verbena officinalis*, *Picris echioides*, *Calystegia sepium*, *Plantago major* and *Cirsium arvense* (Tab. IV). This might have been caused by lower competition, lower herbicide use or no-till practices in sorghum, but information on management details is lacking. However, it indicates that some perennial species are *not* favoured in alfalfa. The suppressive potential of alfalfas against *C. arvense* has already been observed by previous studies (Ominski et al., 1999). Thistles are probably less affected by soil tillage in annual crops compared with other perennial species (due to the ability to regenerate from root fragments). In contrast, they may particularly suffer from the

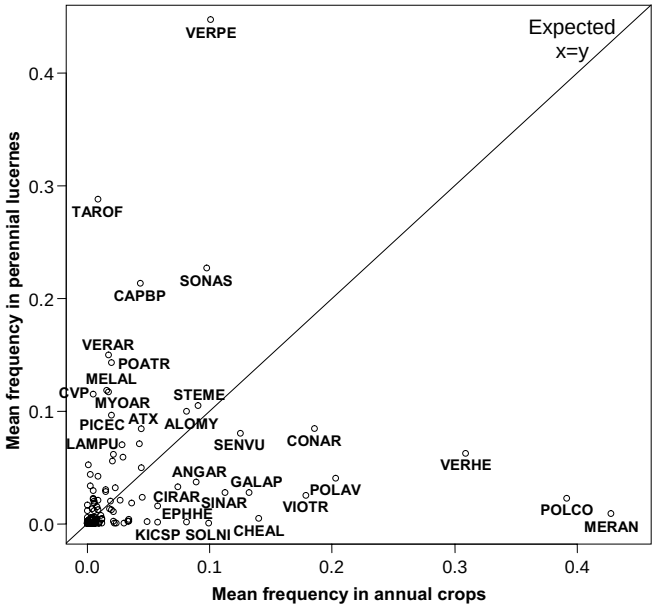

Figure 2. Weed species occurrence in six annual crops (winter wheat, rape, maize, sunflower, pea and sorghum) and in perennial alfalfa crops. Frequency varies between 0 (completely absent in all fields of that group of crops) and 1 (present in all quadrats of all fields). All frequent weed species preferred either annual or perennial crops. SONAS, *Sonchus asper*; STEME, *Stellaria media*; ALOMY, *Alopecurus myosuroides*; ANGAR, *Anagallis arvensis*; ATX, *Atrilex* spp.; LAMPU, *Lamium purpureum*; see Table IV for other species names. Rare taxa are not named in the figure.

high competition and the repeated cuttings in alfalfas depleting their belowground carbohydrate resources needed for regrowth (Graglia et al., 2006).

Besides some perennials including *T. officinale*, *Crepis* spp. and *Silene latifolia*, alfalfas also favoured a few small annual species with a very short life cycle such as *Calepina irregularis*, *C. bursa-pastoris* and *V. persica*. Short life cycles might allow species to produce seeds before the first or between two successive cuttings. Alfalfas might thus generate '*divergent selection pressures*' favouring both long and very short life cycles.

4. CONCLUSION

This study was based on commercial fields from a large area. The advantage of analysing data from real farming systems comes at the cost of various uncontrolled factors (crop management, environmental factors and local weed species pool) that may increase the noise in the data. Despite this noise, we detected strong differences in the weed composition between 6 annual crops and perennial alfalfas. Perennial alfalfas were characterised by reduced abundance of many annual species and some perennials including *Cirsium arvense* that are often problematic weeds in annual crops. In parallel, alfalfas showed increased frequency of some perennial and some short-lived annual species. Several differences between annual and perennial crops including the absence of soil tillage, the increased competition and the frequent hay cuttings may be responsible for these strong weed community shifts. The relative importance of these factors should be determined by more detailed experimental studies.

This strong differentiation of plant communities confirms previous experimental studies and suggests that the diversification of crop rotations with perennial crops could contribute to Integrated Weed Management and herbicide use reduction. While alfalfas hinder the development of several weeds species that are problematic in annual crops, they may maintain a certain abundance and diversity of other wild plant species that may provide trophic resources for animals and other ecosystem services (Gerowitt et al., 2003; Marshall et al., 2003; Holland et al., 2006). The strong impacts of perennial crops on weed communities reported in this paper should be completed by long-term studies tracking the weed community during entire crop rotations.

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C.I.2 **Article 2:**

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Perennial alfalfa affects weed community trajectories in grain crop rotations. *Weed Research* **50**, 331-340.

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Perennial lucerne affects weed community trajectories in grain crop rotations

H MEISS*†, S MÉDIÈNE‡, R WALDHARDT†, J CANEILL*, V BRETAGNOLLE§, X REBOUD* & N MUNIER-JOLAIN*

*INRA, UMR 1210 Biologie et Gestion des Adventices, Dijon, France, †Division of Landscape Ecology and Landscape Planning, Institute of Landscape Ecology and Resources Management, IFZ, Justus-Liebig-University Giessen, Giessen, Germany, ‡AgroParisTech, UMR 211 INRA-AgroParisTech, Thiverval-Grignon, France, and §CEBC-CNRS, Beauvoir-sur-Niort, France

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Summary

Complex crop rotations may be beneficial for weed management. We analysed how pluriannual forage crops may affect weed composition during cereal-based crop rotations. Using a space-for-time-substitution design, we compared weed composition and diversity before, during and after perennial crops. We surveyed four groups of fields: (a) winter wheat (*Triticum aestivum* L.) following annual crops, (b) 1-year old lucerne (*Medicago sativa* L.) following annual crops, (c) 2–6 years old lucerne and (d) winter wheat following pluriannual lucerne in western France (420 fields in total). Weed composition varied among the four groups, suggesting a cyclic trajectory corresponding to the phases of the crop rotation. Indicator Species Analysis showed that these differences were due to at least 40 species, including the most common weeds. A functional group analysis showed that perennial lucerne crops shifted the communities away from several problematic weeds, especially annual broad-leaved species with an upright or climbing morphology. This effect was also visible in the wheat following lucerne. Other species (including perennials, annuals with rosettes and some grasses) benefited from the particular growth conditions in lucerne but decreased in the following wheat. The diversification of arable crop rotations with perennial crops may thus be useful for Integrated Weed Management, reducing the need for herbicides. Other species less harmful to annual crops were favoured, resulting in increased floristic diversity.

Keywords: Integrated Weed Management, crop diversification, temporary grassland, perennial forage crops, *Medicago sativa*, weed functional group, community dynamics.

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Introduction

Most current cropping systems are mainly based on chemical pest and weed control. The sustainability of such systems is questioned more and more because of groundwater pollution, loss of biodiversity, selection of resistance, pesticide residues in food and high economic costs (Nazarko *et al.*, 2005). As a consequence, there is a growing interest in designing cropping systems less reliant on pesticides, including herbicides. It is widely recognised that crop rotation (i.e., temporal crop diversification) may play a significant role in weed management (Liebman & Dyck, 1993; Bellinder *et al.*, 2004; Smith & Gross, 2007; and references therein). Each crop provides specific weed growth conditions, determined by crop-specific characteristics and associated management practices (Doucet *et al.*, 1999), hence acting like a filter determining the assembly of weed

Correspondence: Nicolas Munier-Jolain, Institut National de la Recherche Agronomique, UMR 1210 Biologie et Gestion des Adventices, INRA/AgroSup Dijon/Université de Bourgogne, 17 rue Sully, BP 86510, F-21065 Dijon cedex, France.
Tel: (+33) 380 69 3035; Fax: (+33) 380 69 3262; E-mail: munierj@dijon.inra.fr

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communities (Booth & Swanton, 2002). Growing the same or similar crops in consecutive years would thus favour the same type of weed species in every year. This may reduce weed species diversity, while abundances of a few, well adapted weed species may increase and become problematic. In contrast, rotations of dissimilar crops should favour different weed species types in subsequent years and lower the risk of dense populations of problematic weeds, as suggested by several, mostly experimental, studies (Liebman & Dyck, 1993; Sosnoskie *et al.*, 2006; Smith & Gross, 2007). However, such positive effects may be limited if the rotations are too short or if the included crops are too similar in terms of weed growth conditions.

Besides the introduction of other annual crops or cover crops, rotations may also be diversified by perennial crops lasting several years on the fields including various legumes such as lucerne (*Medicago sativa*), clovers (*Trifolium* sp.), and vetch (*Vicia* sp.); various grasses (*Dactylis glomerata* L., *Lolium* sp., *Festuca* sp.) or legume–grass mixtures (Freyer, 2003). Such crops are usually grown to produce livestock forage in mixed farming systems and for improving soil fertility and crop yields of the following annual crops (Freyer, 2003). They are known as 'temporary grasslands', 'leys', 'sod crops', 'fodder crops', 'hay crops' or even 'cleaning crops' (Liebman & Dyck, 1993; Andersson & Milberg, 1996; Teasdale *et al.*, 2004). While the need and profitability of livestock forage has decreased in some regions, perennial legume or grass crops might increasingly be used for producing energy or raw materials for industry (Tilman *et al.*, 2006).

Several studies suggest that perennial forage crops have strong impacts on weeds (e.g., Andersson & Milberg, 1996; Clay & Aguilar, 1998; Ominski *et al.*, 1999; Schoofs & Entz, 2000; Bellinder *et al.*, 2004; Teasdale *et al.*, 2004; Albrecht, 2005; Heggenstaller & Liebman, 2006; Hiltbrunner *et al.*, 2008). Most of these studies report reduced seed or plant abundances of some major weed species at the end of the perennial crop, despite reduced or no herbicides used in perennial crops (Bellinder *et al.*, 2004), while other species sometimes profited. Several characteristics of perennial crops may contribute to these weed community shifts: (i) the absence of soil tillage for long periods may prevent weed seed germination (Huarte & Arnold, 2003), although it may favour established weeds, especially perennials, (ii) frequent mowing operations (1–5 per year) may reduce weed growth, survival and seed production (Meiss *et al.*, 2008), (iii) however, direct curative weed control actions are often reduced or omitted (Bellinder *et al.*, 2004) and (iv) deep and dense rooting systems and intense canopy closure during the whole vegetative period may create high levels of interspecific competition (Schoofs & Entz, 2000). The impacts and relative importance of these mechanisms are largely unknown.

Nine of the 10 available studies (cited above) investigating the impacts of perennial forage crops on weeds are based on field experiments and are therefore limited in space and time. Typically, 2–4 year rotations were analysed with only 1–2 years of perennial crops. Only one study was based on a larger number of commercial fields from a whole region in Canada (Ominski *et al.*, 1999).

The aim of the present study was to analyse how the insertion of perennial crops into cereal-based rotations affects the weed composition in a realistic situation. We test the hypothesis that weed communities follow a temporal trajectory during the crop rotations, owing to the insertion of perennial corps. We therefore compared the weed species composition, diversity and frequency of functional groups between four key phases of such a long crop rotation: (a) annual crops following annual crops, (b) young perennial crops (year 1), (c) older perennial crops (year 2–6) and (d) annual crops following perennial crops using a space-for-time-substitution design. One strength of our design is the use of weed surveys of a large number of commercial fields and a data set that allowed reconstruction of the rotation history of sampled fields over the last 10 years.

Materials and methods

Study area and sampling design

The study comprised 420 fields randomly distributed in an area of 450 km^2 (containing about 18 000 fields), located in the *Plaine de Niort*, a region of intensive agriculture dominated by cereals with rather fertile and calcareous lime and clay soils in central-western France (46°11′N, 0°28′W). Mean annual precipitation is 779 mm; mean temperature is 12.3°C (5.6°C in winter, 18.9°C in summer). Since the start of the study in 1995, land use (crop species) has been recorded annually and mapped in a Geographical Information System. These data were used to compile the history of the crop sequence of each field.

Four groups of fields were chosen to represent four key stages of a crop rotation including perennial crops, namely: (a) winter wheat following at least 5 years of any annual crops (representing annual crops before the perennial phase), (b) 1-year-old lucerne following several years of annual crops (representing young perennial crops), (c) 2–6 year-old lucerne (representing established perennial crops) and (d) winter wheat following pluri-annual lucerne (representing annual crops after the perennial phase). The four groups (treatments) thus vary

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both by the current crop (wheat vs. lucerne) and the preceding crops (annuals vs. perennials). All surveys were performed during the same season (March to May) of the years 2006, 2007 and 2008. Numbers of fields surveyed per group and per year are provided in Table 1. While most of these fields were chosen independently (space-for-time substitution), some individual fields were followed for the transitions between young and old lucerne (b and c, 13 fields) and between old lucerne and wheat following lucerne (c and d, 12 fields).

Weed species composition was described based on presence–absence data of all herbaceous plant species in several quadrats in each field. Crop volunteers were excluded from all analysis, as they may artificially increase impact of the preceding crop. Lucerne volunteers were frequently found in wheat following lucerne. In wheat, surveys were done in 32 quadrats of 4 m^2 (2 m × 2 m) per field arranged on transects forming an eight-pointed star in the centre of the field. In lucerne, surveys were peformed on 30 quadrats of 0.25 m^2 (0.5 m × 0.5 m) which were arranged on two to three parallel transects. Field edges were avoided in both cases. Different quadrat sizes were necessary to adequately describe the weed species composition in both annual and perennial crops that greatly varied by their vegetation density (high in perennial lucerne, low in winter wheat). A statistical method was used *a posteriori* to check whether the two methods adequately described the weed species composition. For each field, we calculated the ratio of the observed species richness to the expected total species richness estimated by Chao's formula (Colwell & Coddington, 1994) using the 'specpool' function in the 'vegan' package of R 2.8.1 (Oksanen *et al.*, 2009). This ratio was then compared between the four groups of fields. There was no significant variation among mean ($F_{3,416} = 0.67$, $P = 0.57$) and median values ($\chi^2 = 2.2$, $df = 3$, $P = 0.53$) of the four groups. On average, the sampled weed species richness of each field was about 75% of the estimated total, suggesting that both methods were equivalent for describing the weed composition and the relative frequencies of the most important taxa. A total of 161 weed taxa were distinguished, comprising 129 species and 32 genera or species groupings that posed identification difficulties. Presence–absence data of each quadrat were used to calculate the relative frequency of each taxon in the field, which was used as a proxy of the species abundance at the field scale.

Table 1 Four groups of fields (treatments) defined to represent four key stages of crop rotation including annual and perennial crops

		Nb. of fields surveyed			
Group	Crop and precedent	2006	2007	2008	Total
a	Wheat after annual crops	87	41	56	184
b	Lucerne 1 year	14	8	13	35
c	Lucerne 2–6 years	55	53	51	159
d	Wheat after lucerne	4	17	21	42
Total		160	119	141	420

Statistical analysis

Community composition

Rare species (80 taxa present on less than 10 fields out of 420) were excluded from multivariate analysis, as they may unduly influence the results (Kenkel *et al.*, 2002). Canonical Discriminant Analysis (CDA; Kenkel *et al.*, 2002) was used as a constrained ordination method to visualise the differences in weed species composition between the four groups of fields. Analysis of Similarities (ANOSIM; Clarke, 1993) was used for testing differences in species composition. This randomisation-based method is recommended for analysing large multivariate data sets containing many zeroes (Sosnoskie *et al.*, 2006) and does not require assumptions about multivariate normality (Kenkel *et al.*, 2002). We used the Bray–Curtis dissimilarity measure and 10 000 permutations. After the global analysis, we tested the pairwise differences between all groups and reported the Bonferroni-corrected *P*-values. Lastly, Indicator Species Analysis (ISA; Dufrene & Legendre, 1997) was used to identify the most representative weed species of the four groups of fields. Indicator values (IV) are calculated for each species in each pre-defined group varying between 0 (species absent from all fields of that group) and 100 (species present with highest abundances in all fields of the group, thus 'perfect indication'). Indicator values are tested for statistical significance using a randomisation technique (4999 permutations of the field's group memberships).

Functional groups

All 161 weed taxa were sorted into eight *a priori* defined functional groups (FG). Grasses were divided into annual and perennial species, broad-leaved species into annual, perennial and 'intermediate' species (comprising biennials and species varying between annual and perennial life cycles). Annual broad-leaved species constituted the largest group. This was therefore further split according to *morphology*, opposing 'upright' (erect morphology since seedling stage), 'climbing' (species winding on neighbouring plants), 'rosette' (circular arrangement of the first leaves near to the soil surface) and 'other' (comprising all other morphologies). For each field, relative frequencies of the FGs were calculated by dividing the sum of the frequencies of all species in each FG by the sum of species frequencies across all

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functional groups. Mean relative frequencies were square-root transformed to improve the normality of the residuals and compared between the four groups of fields using one-way ANOVA and Tukey *a posteriori* tests.

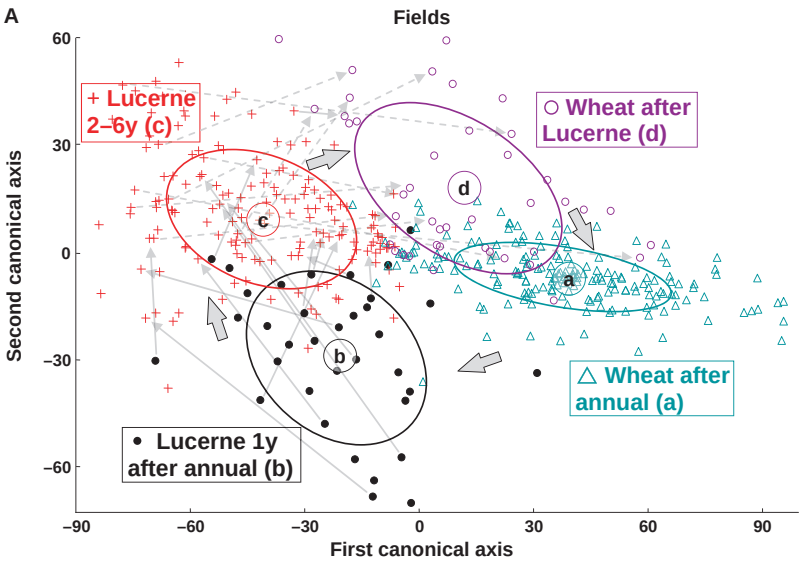
Diversity

We calculated two diversity measures at the field scale (α-diversity), namely the species richness (S) and the Shannon diversity index ($H' = -\Sigma_i p_i \times \ln\ p_i$, with $p_i = n_i/N$, where n_i is the relative frequency of species i and N the sum over all species). One-way ANOVA and Tukey tests were used to compare these two measures between the four treatments. The Bray–Curtis distance of each field from the group centroids in multivariate space was used as a measure of dissimilarity between fields (β-diversity) at the group scale (see Anderson *et al.*, 2006). This measure is independent of group size, which was quite variable (Table 1). It was calculated using the 'betadisper' function of the 'vegan' package of R (Oksanen *et al.*, 2009). Pairwise comparisons between the four treatments were done by using the permutation-based test of 'multivariate homogeneity of group dispersions' in the 'vegan' package.

Results

Community composition and diversity

The weed species composition differed strongly among the four groups of fields representing key stages of the crop rotation (ANOSIM-R = 0.42, $P < 0.0001$) resulting in a circular formation on the first two CDA axes



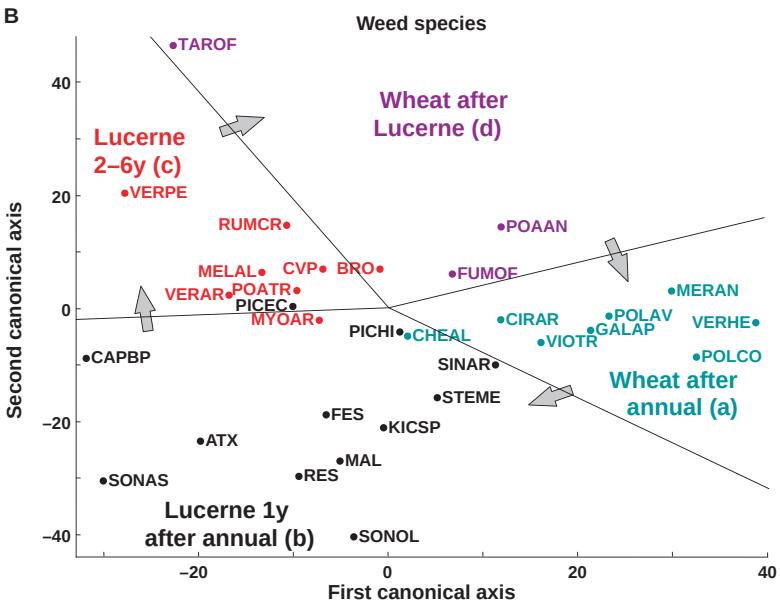


Fig. 1 Canonical Discriminant Analysis (CDA) of weed communities in four groups of fields representing key stages of a crop rotation (see Table 1). Broad arrows indicate the cyclic succession of the weed community during the crop rotation. (A) Relevés at the field scale: (a) △ wheat following annual crops, (b) ● 1 year lucerne following annual crops; (c) +2–6 year lucerne and (d) ○ wheat following pluriannual lucerne. Each symbol corresponds to one randomly chosen field (N = 420 fields), fine arrows indicate successions of individual fields between groups b–c (—) and c–d (- - -). (B) Weed species (see Table 3 for species codes). Only species with $IV_{max} \geq 15$ and $P < 0.05$ (Table 3) are shown.

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(Fig. 1A). The order of the four groups of fields (a–d) corresponds to the order of the phases during the crop rotation and thus to the hypothetical temporal trajectory of weed communities. The cyclic trajectory of weed communities was also confirmed by following the individual fields of young and old lucerne and wheat following lucerne in subsequent years (Fig. 1A). Pairwise comparisons showed that weed species composition differed significantly between all treatments (Table 2). Differences were greatest between wheat following annual crops (group a) vs. 2–6 year old lucerne (c) (Table 2). In CDA, these two groups were mainly separated on the first axis (Fig. 1A). The second highest difference appeared between first-year lucerne (b) and wheat following lucerne (d), which was mainly separated on the second CDA axis. Differences were thus stronger between groups lying on opposite sides of the circle and lower, but still significant, between adjacent groups, which would follow each other in the rotation (Table 2, Fig. 1A).

Indicator Species Analysis (ISA) showed that nine weed species were significantly associated with wheat following annual crops (a) (see Table 3). First-year lucerne (b) was associated with 16 other species, while most of the 9 species typical for wheat after annual crops had reduced Indicator Values. As a result, species richness and Shannon diversity indices at the field scale (α-diversity) were increased and young lucerne had also a higher dissimilarity between the fields (β-diversity) than wheat following annual crops (Fig. 2). Older lucerne (c) was significantly associated with 10 species and four additional species had similarly high IV in young and old lucerne (Table 3). In contrast, most weed species that were typical of annual crops had further reduced frequencies or disappeared. As a result, mean α-diversity dropped down again to the level of annual crops (about 20 species per field), while mean β-diversity remained high (Fig. 2). Only four species showed highest IV in wheat following perennial lucerne (d), but IV of some species were nearly the same as in group c, demonstrating the similarity between old lucerne and the following annual crops. On the contrary, wheat following lucerne also contained several species typical for annual crops, but always with lower IV (see Table 3). Interestingly, none of the three diversity measures differed between old lucerne and the following wheat; β-diversity was thus significantly higher than in wheat following annual crops (Fig. 2). The weed species which were significant in ISA ($P < 0.05$ and $IV_{max} \geq 15$) are represented on the CDA plot illustrating the trajectories of individual weed species during the crop rotation (Fig. 1B).

Table 2 Pairwise comparisons of weed communities in four crop treatments (Table 1). ANOSIM-R varies between 1 (groups do not share any species) and 0 (no differences between groups) (Clarke, 1993)

Contrast	ANOSIM-R
(c) Lucerne 2–6 years vs. (a) wheat after annuals	0.326****
(b) Lucerne 1 year vs. (d) wheat after lucerne	0.171****
(c) Lucerne 2–6 years vs. (d) wheat after lucerne	0.109****
(b) Lucerne 1 year vs. (a) wheat after annuals	0.107****
(b) Lucerne 1 year vs. (c) lucerne 2–6 years	0.062****
(a) Wheat after annuals vs. (d) wheat after lucerne	0.045****

****$P < 0.0001$ (Bonferroni-corrected).

Functional groups

Relative frequencies of the *a-priori* defined weed FG varied between the four treatments. Differences were significant for six out of the eight FG (Fig. 3). Relative frequencies of both upright and climbing annual broad-leaved species (FG 1 and 2) were highest in wheat after annual crops (a), reduced in young lucerne (b), more strongly reduced in old lucerne (c), and increased again in wheat after annual crops (d), though they did not reach the level of (a). The opposite pattern was observed with four other FG: annuals with rosettes, broad-leaved species with 'intermediate' life cycles, perennial broad-leaved species and perennial grasses (FG 4, 5, 6 and 8), which were two to three times more frequent in old lucerne (c) than in wheat after annual crops (a). Two FG did not show any significant difference: annual broad-leaved species with 'other' morphologies (FG 3) and annual grasses (FG 7) (see Fig. 3).

Discussion

This study indicates that weed community dynamics are strongly affected by perennial lucerne. In accordance with Ominski *et al.* (1999), wheat fields following pluriannual lucerne (d) vs. several years of annual crops (a) showed strong differences in weed species composition. These differences were consistent with, and may thus be explained by, the weed community trajectories during the perennial crops (b and c), which, to our knowledge, have not been shown to date. Below we compare the observed community shifts to findings in previous studies and discuss possible underlying mechanisms.

Lucerne had strong negative impacts on broad-leaved weeds with an upright morphology (FG 1, e.g. *Mercurialis annua* L., *Chenopodium album* L., *Solanum nigrum* L.) and on species climbing on neighbouring plants (FG 2, e.g. *Galium aparine* L., *Fallopia convolvulus* (L.) Á. Löve). In previous studies, species with similar morphologies, including *Abutilon theophrasti* Medik., *Amaranthus* sp., *C. album*, and *G. aparine*, reacted in a similar way

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Table 3 Indicator Species Analysis (ISA) of the four groups of fields (a–d) representing key stages of the rotation (Table 1)

Weed species	Code	Group (treatment) (a) Wheat after annuals	(b) Lucerne 1 year	(c) Lucerne 2–6 years	(d) Wheat after Lucerne	*P*-value
Indicators of wheat after annuals (a)						
Mercurialis annua	MERAN	**30**	6	0	**25**	0.0008
Veronica hederifolia	VERHE	**35**	9	2	**25**	0.0002
Fallopia convolvulus	POLCO	**40**	12	1	**26**	0.0002
Galium aparine	GALAP	**32**	10	2	13	0.0004
Polygonum aviculare	POLAV	**32**	9	2	19	0.0010
Viola arvensis + tricolor + sp.	VIOTR	**28**	9	1	15	0.0022
Chenopodium album	CHEAL	**20**	5	0	16	0.0134
Cirsium arvense + sp.	CIRAR	**22**	9	6	6	0.0196
Solanum nigrum + sp.	SOLNI	10	0	0	1	0.0156
Indicators of lucerne 1 year (b)						
Stellaria media	STEME	10	**24**	7	11	0.0120
Sinapis arvensis	SINAR	17	19	1	4	0.0418
Sonchus oleraceus	SONOL	0	**38**	2	1	0.0002
Reseda lutea + sp.	RES	0	**31**	0	0	0.0002
Kickxia spuria + sp.	KICSP	2	**24**	1	0	0.0002
Malva neglecta + sylvestris + sp.	MAL	0	19	5	0	0.0004
Festuca rubra + sp.	FES	0	15	1	0	0.0004
Lamium amplexicaule	LAMAM	3	15	5	6	0.0470
Lapsana communis + sp.	LAPCO	1	14	0	0	0.0044
Atriplex patula + prostrata + sp.	ATX	1	**40**	10	0	0.0002
Picris echioides	PICEC	0	**27**	17	1	0.0004
Picris hieracioides	PICHI	3	17	15	0	0.0266
Sonchus asper	SONAS	1	**51**	**23**	4	0.0002
Capsella bursa-pastoris	CAPBP	1	**33**	**32**	0	0.0004
Lactuca serriola	LACSE	1	18	18	0	0.0092
Calepina irregularis	CPAIR	0	12	12	0	0.0236
Indicators of lucerne 2–6 years (c)						
Veronica arvensis + polita	VERAR	1	14	17	9	0.0270
Crepis sancta + vesicaria + sp.	CVP	0	7	**30**	2	0.0002
Poa trivialis	POATR	2	4	**20**	8	0.0098
Bromus sterilis + mollis + sp.	BRO	2	5	19	6	0.0210
Rumex crispus	RUMCR	0	5	18	3	0.0046
Myosotis arvensis + sp.	MYOAR	2	9	17	8	0.0472
Cerastium arvense + glomeratum	CER	0	2	13	5	0.0174
Geranium rotundifolium	GERRT	1	2	13	0	0.0210
Silene latifolia	MELAL	0	15	18	15	0.0484
Veronica persica	VERPE	7	17	**35**	**24**	0.0002
Indicators of wheat after lucerne (d)						
Taraxacum officinale	TAROF	0	4	**34**	**39**	0.0002
Poa annua	POAAN	4	0	3	**27**	0.0006
Falcaria vulgaris	FALVU	1	0	2	11	0.0198
Fumaria officinalis + sp.	FUMOF	15	2	0	18	0.0136

High indicator values (IV) are shaded in darker grey with three levels: IV ≥ 10, IV ≥ 20 and IV ≥ 30. They appear mostly in one or two adjacent groups of fields, showing that the weed species are not randomly distributed but follow a trajectory during the long crop rotation. Only weed species with $IV_{max} \geq 10$ and $P < 0.05$ are shown.

(Ominski *et al.*, 1999; Teasdale *et al.*, 2004; Albrecht, 2005; Heggenstaller & Liebman, 2006). Upright and climbing broad-leaved plants may be particularly vulnerable to frequent cutting removing large parts of leaves and also buds/meristems needed for resprouting. Therefore, such plant types are likely to have slowest regrowth and highest mortality rates in frequently cut crops, such as lucerne. In contrast, cutting may cause less damage in broad-leaved species with rosettes and in grasses, since buds and leaves are located nearer to the soil surface. This mechanism has been suggested by experiments on individual plants (Meiss *et al.*, 2008). The present study is, to our knowledge, the first one testing this hypothesis for weed communities in real fields.

Our results also indicate that lucerne favours perennial broad-leaved species. Increased occurrences of the

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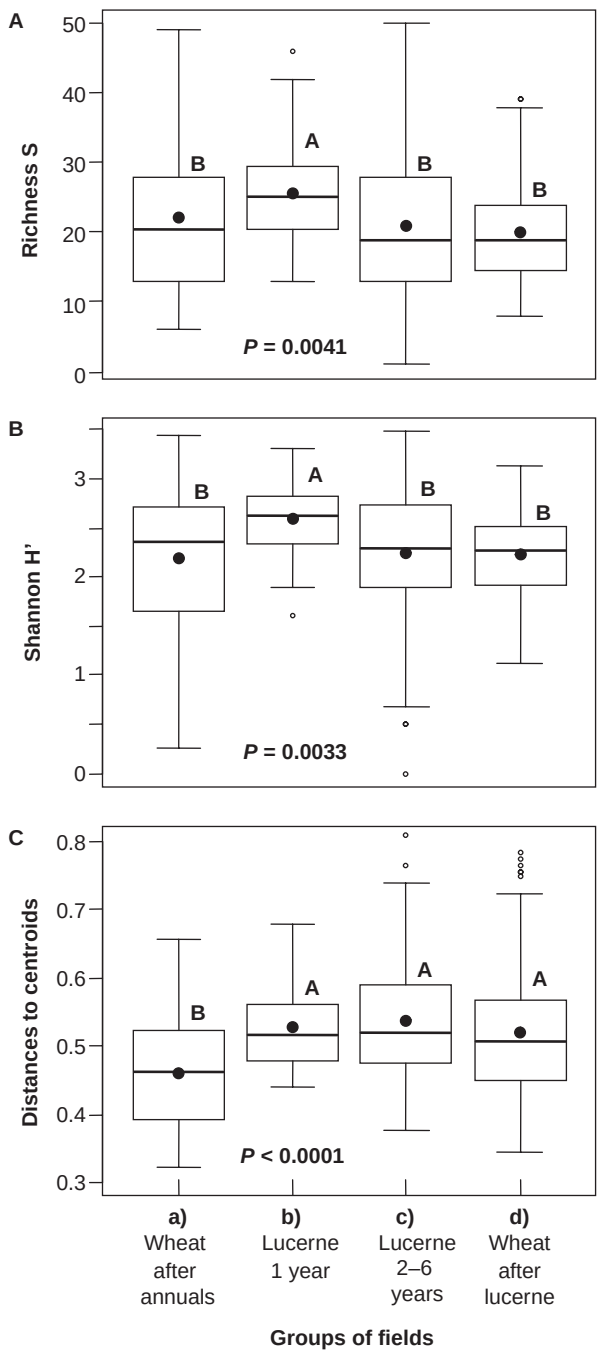

Fig. 2 Weed species diversity measures for four groups of fields (see Table 1). (A) species richness (B) Shannon diversity index, (C) Bray–Curtis distance to group centroids (beta-diversity). Broad lines are medians, black dots are means, boxes show the inter-quartile range and whiskers extend to the last data point within 1.5 times the inter-quartile range, open circles are further outliers. *P*-values of ANOVA (A, B) and permutation tests (C) are given. Groups not sharing the same letter are significantly different at $\alpha = 0.05$.

perennials *Taraxacum* spp. and *Rumex* spp. have already been reported (Ominski *et al*., 1999; Albrecht, 2005; Hiltbrunner *et al*., 2008; Ulber *et al*., 2009). Our surveys suggest that other perennial species/genera react similarly (*Reseda* spp., *Malva* spp., *Picris* spp., *Crepis* spp., *Silene latifolia* Poir., *Falcaria vulgaris* Bernh., Table 3), leading to a strong response of the whole functional group (Fig. 3). Perennial species likely profited from the absence of soil tillage. In this way, weed growth conditions in pluriannual lucerne may be similar to no-till systems (e.g. Zanin *et al*., 1997). Some perennials might also be more tolerant to prolonged competition. Conversely, most annual weeds are probably best adapted to annual crops and survive the yearly soil tillage as seeds in the soil. Soil tillage may even promote recruitment of annual weeds, while it may be inhibited under dense canopies of perennial crops (Huarte & Arnold, 2003). Annual crops would therefore correspond to very early successional stages favouring r-selected species with shorter life cycles and generative reproduction (therophytes), whereas established lucerne would correspond to later successional stages favouring slower growing and longer living biennial and perennial (K-selected) species (hemicryptophytes and geophytes). *Cirsium arvense* (L.) Scop. was the most important exception (Table 3), despite its perennial life cycle. Negative impacts of forage crops on *C. arvense* have repeatedly been observed (e.g., Ominski *et al*., 1999) and might be linked to the repeated mowings exhausting the carbohydrate reserves needed for regrowth (Graglia *et al*., 2006).

While the *a priori* division of broad-leaved species into six functional groups according to life cycle and morphology has proven to be quite successful in our study, we have no explanation for the heterogeneous reactions of the different grass species. Grasses may show a better regrowth after cutting than broad-leaved species, but cutting may strongly reduce seed production, especially of tall grasses. In previous studies, some grass species including *Apera spica-venti* (L.) P.Beauv., *Avena fatua* L. and *Setaria faberi* F.Herm. were suppressed by forage crops (Schoofs & Entz, 2000; Albrecht, 2005), while others including *Elymus repens* (L.) Gould and *Poa* sp. increased (Andersson & Milberg, 1996; Clay & Aguilar, 1998; Teasdale *et al*., 2004; Albrecht, 2005). In our study, the FG of perennial grasses was slightly increased in lucerne, which may be compared with the positive reaction of perennial broad-leaved species (see above). In contrast, the FG of annual grasses showed no significant differences. Looking at each individual species might be more informative. Species favoured by lucerne included both perennial and annual grasses (*Poa trivialis* L. and *Bromus* spp.) and some species that are sometimes included in the sown mixtures (*Lolium* spp. and *Festuca* spp., Andersson & Milberg, 1996), while other annual and perennial grasses showed no differences or were suppressed (*Alopecurus myosuroides* Hudson., *A. fatua*, *P. annua* and *E. repens*).

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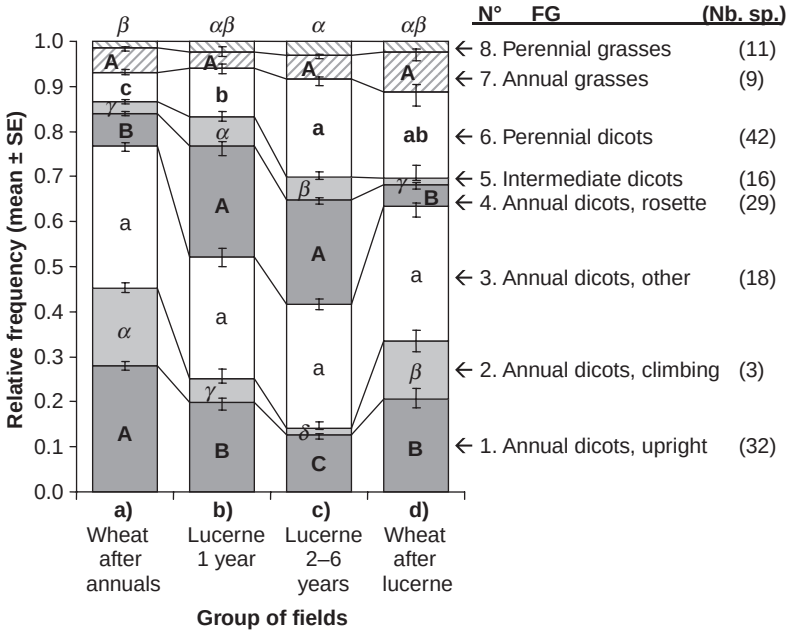

Fig. 3 Relative frequencies of eight functional groups (see Methods) of weed species in four groups of fields (a–d) representing key stages of the rotation (Table 1). The graph shows mean relative frequencies of each FG and standard errors *inside* of each boundary. Dicots, broad-leaved species; intermediate, biennial or facultative perennial species; upright, erect morphology; climbing, winding on neighbouring plants; rosette, circular arrangement of the first leaves near to the soil; other, all other morphologies; Nb.sp., numbers of weed species in the FG. Mean frequencies not labelled by the same letter are significantly different between the treatments.

Impacts on grasses may particularly depend on the exact crop management history (sowing and cutting dates) of each individual field, which was not available for this large scale study.

Results from Indicator Species Analysis (Table 3) widely agreed with the analysis of functional groups (Fig. 3). These two methods are complementary: while ISA allows testing the reaction of individual species, analysis of FGs allows inclusion of information on *all* taxa, including the large number of rare taxa (80 out of 161 taxa). Nevertheless, groups containing only a few species, such as FG 2, showed clearer differences between the treatments (Fig. 3). More narrowly defined FG or trait-based analysis might thus be useful to further investigate the differences between the weed species.

Weed community changes in perennial lucerne are most likely due to the absence of soil tillage, reduced chemical weed control, temporally extended competition and frequent hay cuttings. However, perennial crops may also have other, more indirect, impacts on weeds. The reduced belowground disturbances and the permanent vegetation may modify the soil characteristics (organic matter, humidity, and nutrient availability) and microclimatic conditions (temperature, light quantity and quality) (Huarte & Arnold, 2003). Perennial crops may also favour the accumulation of plant litter on the soil surface, creating a weed suppressing mulch. Finally, perennial crops may favour weed seed predation by animals, since weed seeds stay longer on the soil surface (no soil tillage) and the permanent vegetation cover may constitute a favourable foraging habitat for seed predators (Heggenstaller *et al.*, 2006). Perennial crops may thus correspond to several filters (*sensu* Booth & Swanton, 2002) with varying effects on different weeds. In contrast, weed communities in most annual crops are probably selected by a few rather strong and uniform filters such as herbicides and annual soil tillage. This is consistent with the increased dissimilarity (β-diversity) among the lucerne fields (b and c) and among the wheat following lucerne (d) (Fig. 2).

Using data on expressed weed communities and the crop rotation histories of a large number of commercial fields made our study as realistic as possible. This advantage over local field experiments comes at the cost of having various uncontrolled factors linked to the crop management, environmental variables and local weed species pools, increasing the noise in the data. Nevertheless, we detected significant differences in weed species composition associated with the inclusion of perennial lucerne in the crop rotations. Reduced frequencies of several weed species that are typical (and problematic) in annual crops suggest a possible use of perennial lucerne for preventive weed management. Increased occurrences of broad-leaved species (perennials and annuals with rosettes) in and after lucerne are not likely to be problematic in annual crops. Most of them already had strongly reduced abundances in wheat following lucerne (except *T. officinale* and *V. persica*) and were very rare in, or absent from, the established vegetation in wheat following annual crops (Table 3). Potential agronomical problems might rather result from some grasses, even though grasses constituted only small parts of the weed communities in all treatments (Fig. 3). Some grass species (*B. sterilis*, *A. myosuroides*) might be favoured both in winter cereals and in mown perennial forage crops. Therefore, rotations should also

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contain spring/summer sown crops, where such problematic grasses are not adapted (Chauvel *et al*., 2001).

The strong weed community shifts observed in the space-for-time substitution study had to be confirmed by classical crop rotation experiments. In particular, future (long term) studies should analyse the duration of the effect of perennial crops and determine whether, and after how many years of annual crops, weed communities move again to the (initial) state (a), closing the cyclic trajectory or not. In a Canadian survey, farmers estimated that weed control benefits of perennial forage crops lasted for one, two, three or more years (11%, 50% and 33% of respondents, respectively) (Entz *et al*., 1995).

Results of this study suggest that the inclusion of perennial crops into cereal-based crop rotations may reduce the abundances of weeds that are problematic in annual crops while favouring other less problematic species. These species may provide food resources for heterotrophic organisms and other ecosystem services that are increasingly recognised (Gerowitt *et al*., 2003; Marshall *et al*., 2003). Changes in weed community composition provoked by the diversification of crop rotations with perennial crops may thus (i) contribute to Integrated Weed Management reducing the need for herbicide applications and (ii) alleviate the trade-off between agricultural production and the conservation of farmland biodiversity.

Acknowledgements

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C.II EXPERIMENTAL ANALYSES OF THE IMPACTS OF TEMPORARY GRASSLANDS ON WEED POPULATIONS

This second empirical chapter of the thesis has not been submitted for publication so far. The current status of this chapter is 'article in preparation'. The chapter is presented as one single text to avoid redundancies, but it will later probably be divided into two articles.

Manuscript 3:

H Meiss, R Waldhardt, J Caneill, N Munier-Jolain (in preparation)

Mechanisms affecting population dynamics of weeds in perennial forage crops.

Abstract

Perennial forage crops may have very strong impacts on weed communities, as suggested by weed surveys on commercial fields and field experiments. However, little is known about the mechanisms causing such impacts and many previous studies confounded the crop treatments with herbicide treatments. In a 2.5-years field experiment, population dynamics of 16 artificially sown and other naturally occurring weed species were compared between perennial forage crops and a succession of annual cereal crops both with contrasted management options but always without herbicides. Perennial crops differed by crop species (*Medicago sativa vs. Dactylis glomerata*), sowing season (autumn *vs.* spring) and cutting frequency (3 *vs.* 5 cuts per year). The succession of annual crops (winter wheat–intercrop–spring barley–intercrop) differed by the intercrop treatment (with or without autumn soil tillage and with or without a mustard cover crop).

Total weed plant densities and aboveground crop and weed biomasses were measured every 1-3 month during the whole vegetation period. Both showed decreasing tendencies in all treatments of perennial crops but increasing tendencies in the succession of annual crops. Species richness showed the same tendencies but the richness/abundance ratios improved with time in perennial crops and deteriorated in the annual crops. At the end of the experiment, the weed community composition differed most strongly between annual and perennial crop treatments. This was mainly caused by strong weed population increases of *G. aparine, A. myosuroides* and other annual weed species in all annual crop treatments. Among the

perennial crop treatments, differences between spring and autumn sown crops were much stronger than between the two cutting frequencies and the two crop species.

Results suggested that several stages of the weed life cycle were affected by three main characteristics of perennial forage crops :

A) The absence of soil tillage was probably the main reason for i) reduced germination and emergence rates in the perennial crops after the crop establishment phase, ii) increased survival of established weed plants and probably also iii) reduced weed seed survival, as seeds stay on the soil surface.

B) The strong and temporally extended competition of the perennial crops reduced vegetative weed growth and seed production.

C) The frequent hay cuttings destroyed the shoots and reduced seed production of weed plants that often showed lower regrowth and higher mortality rates than the perennial forage crops. In contrast, weeds were not able to profit from temporally reduced competition for light after hay cuttings.

The rather complex experimental design and the frequent observation dates permitted disentangling some, but not all, of these mechanisms that acted often simultaneously, showed reinforcing or compensating interactions and cumulative effects on the weed life cycle.

Key words: Plant population dynamic, temporary grassland, crop rotation, soil tillage, competition, cutting, regrowth, Integrated Weed Management, biodiversity.

C.II.1 Introduction

Today's crop rotations are frequently very short (2-4 years) and often constituted by crops that provide rather similar weed growth conditions (*e.g.* only annual winter-sown crops). Therefore, weed species adapted to the conditions in these crops may be favoured in every year leading to high population growth rates which increases the need of intensive curative (chemical or mechanical) weed control. However, these techniques may have strong negative environmental side effects which are increasingly considered (*e.g.* groundwater pollution by

herbicides, soil erosion due to intensive soil tillage, reduced carbon fixation and increased CO_2-emissions). Intensive chemical and mechanical weed control may also have negative effects on different elements of farmland biodiversity, either by direct destruction of organisms or by alternating the food availability and habitat quality (Semere and Slater, 2007). Both mechanical and chemical weed control may have very high economic costs and need a lot of non-renewable resources. Finally, the long-term efficiency of herbicides is also questioned due to the appearance of herbicide resistant weed biotypes. All these reasons increased the need for developing more sustainable weed management systems.

The diversification of crop rotations may be an important element to achieve this goal. In alternating the selection pressures, it may prohibit strong population increases of particular weed species, which may be the case in monocultures. It is frequently cited as an important element of IWM (Liebman and Dyck, 1993; Buhler, 2002; Cardina *et al.*, 2002a; Nazarko *et al.*, 2005). Crop rotations may be diversified either by introducing additional annual cash crops, by growing 'cover' or 'catch' crops in the period between successive cash crops, but also by introducing perennial crops lasting several years on the fields. In central Europe, perennial crops consisting of grasses, legumes or mixtures were widely used for livestock forage production in mixed farming systems (perennial forage crops, PFCs) but the importance of these systems declined during the last 60 years (Freyer, 2003). However, perennial crops recently gained new interest for sustainable farming design as they may increase soil organic matter and carbon storage important for the global climate, improve soil fertility, which may have positive effects on crop yields and may reduce fertilizer inputs, especially after perennial legume crops, reduce soil erosion and nitrogen leaching and increase the landscape heterogeneity, biodiversity and associated ecosystem services (Katsvairo *et al.*, 2006b). Perennial crops have recently gained new interest for the production of bio-energy and other renewable resources (Tilman *et al.*, 2006; Ceotto, 2008).

The (re-)introduction of perennial crops into arable crop rotations may also cause benefits for weed management. Perennial and annual crops differ in numerous aspects that may be important for weeds. PFCs are *e.g.* characterized by (a) the complete absence of soil tillage and sowing operations during several years, (b) permanent vegetation that is present nearly all year round, but (c) several hay cuttings per year regularly destroying large parts of the aboveground biomass of crops and weeds. In contrast, most annual crops are characterized by annual soil tillage and sowing operations, the crop vegetation is only present during shorter periods of the year and they are harvested only once per year. These modified conditions in

PFCs might inhibit the successful germination, growth and reproduction of weed species that are adapted to annual crops but may favour the growth of other species at the same time resulting in plant community shifts. Such community shifts were observed in a large-scale weed surveys in Canada (Ominski *et al.*, 1999) and recently in France (Meiss *et al.*, 2010a; Meiss *et al.*, 2010b) and are also suggested by several field experiments (reviewed in Meiss *et al.*, 2010a).

Understanding the mechanisms involved in the observed effects is necessary for generalizing the results, for understanding the potential antagonistic observations reported by some authors, and for developing predictive models. Previous experiments frequently confounded the differences between annual and perennial crops (cited above) with differences in herbicide treatments, as PFCs are frequently characterized by reduced herbicide treatments or the use of herbicides with other active ingredients (Summers, 1998; Meiss *et al.*, 2010a). However, besides the strong and rather well-known effects of herbicides, many other differences between annual and perennial crops may impact the weed species composition, that are not well understood.

In this manuscript, it will first be analyzed which weed species are favoured and suppressed in annual and perennial crops. Then, the impacts of contrasted crop management options will be analyzed (including crop species, sowing date and cutting frequency in the perennial crops and management options of the intercrops between successive annual crops). Finally, these results will be used to investigate and discuss the underlying mechanisms of the impacts on weeds.

A 2.5-year field experiment was set up to compare the population dynamics of different common annual weed species between PFCs and a succession of annual crops. For the perennial crops, six crop management treatments were compared that differed by three factors: **1)** the **crop species**, opposing a legume and a grass crop, which differ *e.g.* in establishment and growth dynamics, symbiotic nitrogen fixation and fertilisation, hence affecting crop-weed competition and other weed growth conditions; **2)** the **sowing date**, opposing autumn and spring sowing, which is known to affect weed recruitment in annual crops (Hald, 1999); and **3)** the crop **cutting frequency**, which may have strong impacts on weed plant survival and seed production. These three factors were partially combined in order to create a variety of weed growth conditions. These perennial crop treatments were compared to a succession of annual cereal crops which differed in various aspects to the perennial crops including soil tillage, crop growth dynamics, and harvesting dates (only one cereal harvest per year). For the

succession of annual crops, three intercrop management options were compared, namely i) conventionally tilled intercrops with bare soil in winter, ii) tilled intercrops with a cover crop in winter (used to reduce nitrogen leaching) that may also change the weed growth conditions (Liebman and Davis, 2000; Moonen and Barberi, 2004) and iii) untilled overwinter stubble fields (OSFs) corresponding to an agri-environment scheme where the soil is only tilled at the end of winter (Critchley *et al.*, 2004; Marsall *et al.*, 2007). In such OSFs, established weed plants may benefit from the absence of soil tillage (as in perennial crops) but also from the limited inter-plant competition, which may increase their seed output. This agri-environment scheme may be favourable to farmland biodiversity, as plant residues and seeds remain at the soil surface where it may be eaten by animals (Moorcroft *et al.*, 2002; Orlowski, 2006).

This experimental design was used to analyse the temporal dynamics of the emerged weed communities during the whole experimental period, concentrating on weed species composition, weed plant densities, and biomass. Finally, the potential underlying mechanisms are discussed, based on the weed population dynamics in the different experimental treatments.

C.II.2 Methods

C.II.2.1 Experimental design

The field experiment was located at the experimental farm 'Epoisses' of INRA-Dijon in eastern France (47°20'N, 5°20'E) with a semi-continental climate and a calcareous clayey soil. Nine crop treatments were compared (T2-T11, see Table 6 for details). Treatments varied first by the crop type, opposing a succession of annual crops: winter wheat (*Triticum aestivum*)–spring barley (*Hordeum vulgare*)–summer soybean (*Glycine max*) and two PFCs: alfalfa/lucerne (*Medicago sativa*) and cocksfoot/orchard grass (*Dactylis glomerata*). Within the perennial crops, treatments further varied by crop sowing season, opposing autumn sowing (4 Sept. 2006) and spring sowing (27 April 2007), and by cutting frequency, opposing a high frequency (5 cuttings per year, C+) and a low frequency (3 cuttings per year, C-) for the autumn sown plots. Sowing and cutting dates are given in Table 6, lower part. Cuttings were performed at about 3-8cm height from soil surface using a forage mower adapted to the small experimental plots that directly removed the cut biomass. Within the succession of annual crops, three intercrop treatments were compared: treatment T9 with superficial soil tillage (5-8cm) performed with a rotary hoe '*rotavator*' after crop harvest ('conventional', bare soil

during winter), T10 without soil tillage after crop harvest (overwinter stubbles), and T11 with superficial soil tillage after harvest and mustard (*Sinapis alba*) grown as a cover crop during autumn/winter (see Table 6 for tillage and sowing dates). All annual crop treatments received superficial soil tillage prior to each sowing. In contrast to most of the previous studies, herbicides were not used in any crop. Mineral nitrogen fertilizers were used in the annual crops and in cocksfoot, but not in alfalfa (see Table 6). Fertilizer application rates, sowing dates and sowing densities followed local farm recommendations. Each of the nine crop treatments was replicated 4 times in a complete bloc design. Plots were randomly distributed on the experimental field except the plots of the two spring-sown perennial crops. For practical reasons, these treatments formed one separate block on the North-East of the experimental (Fig. 10). Plot size was 75m² (7.5 m × 10 m), and each plot was composed of 6 adjacent micro-plots (7.5 m × 1.5 m, illustrated in Fig. 10).

Table 6: Characteristics of nine crop treatments (T2-T11).

A) Upper part: Crop management details.

ID	Crop		Crop management			Intercrop management	
	Type	Species	Sowing season	Fertilisation	Cutting frequency	Autum soil tillage	Cover crops (mustard)
T2	Per	*M. sativa*	Autumn 06	No	C- (3/year)	/	/
T4	Per	*M. sativa*	Autumn 06	No	C+ (5/year)	/	/
T5	Per	*M. sativa*	Spring 07	No	C+ (5/year)	/	/
T6	Per	*D. glomerata*	Spring 07	Yes	C+ (5/year)	/	/
T7	Per	*D. glomerata*	Autumn 06	Yes	C+ (5/year)	/	/
T8	Per	*D. glomerata*	Autumn 06	Yes	C- (3/year)	/	/
T9	Ann	W-B	See below	Yes	1/year	Yes (T+)	No
T10	Ann	W-B	See below	Yes	1/year	No (T-)	No
T11	Ann	W-B	See below	Yes	2/year	Yes (T+)	Yes (M)

B) Lower part: Soil tillage, sowing, and cutting dates.

ID	Crop type	2006						2007										2008									2009	
		1/9	4/9	4/9	6/9	2/10	5/10	5/3	13/3	27/4	7/6	13/7	19/7	1/8	31/8	4-24/10	28/10	13/11	30/1	23/2	29/4	29/5	10/7	30/7	29/8	12/11	?/12	?/1	24/4
T2	Per	T	S_w	S	I					C		C				C						C			C	C			
T4	Per	T	S_w	S	I					C	C	C			C	C					C	C	C		C	C			C
T5	Per	T	S_w		I			T	T	S		C			C	C					C	C	C		C	C			C
T6	Per	T	S_w		I			T	T	S		C			C	C					C	C	C		C	C			C
T7	Per	T	S_w	S	I					C	C	C			C	C					C	C	C		C	C			C
T8	Per	T	S_w	S	I					C		C				C						C			C	C			
T9	Ann	T	S_w		I	T	S						C	T			T		T	S				C	T			T	
T10	Ann	T	S_w		I	T	S						C						T	S				C			?	T	
T11	Ann	T	S_w		I	T	S						C	TS				T	T	S				C	TS		T	T	

Per, perennial crops; Ann, succession of annual crops, W-B, winter wheat followed by spring barley; C, forage cutting or cereal harvest; S, sowing (crops); S_w, sowing (weeds); T, superficial soil tillage (5-8 cm) with a rotary hoe '*rotavator*'; I, irrigation (35mm).

C.II.2.1.1 Weed seed addition

At the beginning of the experiment (4 Sept. 2006), the natural soil seed bank was supplemented by sowing 17 common annual weed species representing 13 families (see Table 7 for species names). Species were selected among the most common arable weeds in France but excluding wind dispersed species to reduce dispersion and contamination of neighbouring plots. Weed seeds were provided by 'Herbiseed', Twyford, Berkshire, UK (http://www.herbiseed.com). Weed seeds were sown prior to crop sowing using a specialized sowing machine and slightly incorporated in the soil (0-5cm deep). Sowing density varied between 8 and 45 seeds per m² (mean=30) depending on the species (see Table 7) giving a total of about 500 weed seeds added per m². One out of the six micro plots of each plot was left unsown for control ('unsown zone f' on Fig. 10).

Table 7: Weed species sown on the experimental plots.

Scientific Name	Code	English name	Family	D	G	V	R
				m^{-2}	% ±SD		%
Alopecurus myosuroides Huds.	ALOMY	blackgrass	Poaceae	30.4	52±15	67±12	27.6
Amaranthus retroflexus L.	AMARE	common amaranth	Amaranthaceae	45.4	93±5	98±4	1.8
Anagallis arvensis L.	ANGAR	scarlet pimpernel	Primulaceae	42.0	43±48	95±8	1.9
Bromus sterilis L.	BROST	barren brome	Poaceae	25.0	95±8	95±8	10.4
Capsella bursa-pastoris Medi	CAPBP	shepherd's-purse	Brassicaceae	33.6	20±13	NA	11.5
Chenopodium album L.	CHEAL	fat hen	Chenopodiaceae	29.2	82±13	92±8	1.6
Fallopia convolvulus (L.) Å. Löve	POLCO	black bindweed	Polygonaceae	32.8	0±0	58±15	10.3
Galium aparine L.	GALAP	cleavers	Rubiaceae	7.5	10±15	42±12	42.1
Geranium dissectum L.	GERDI	cut-leaved crane's-bill	Geraniaceae	14.0	58±32	93±10	29.3
Lamium purpureum L.	LAMPU	red dead-nettle	Lamiaceae	30.0	00±0	60±18	0.9
Lolium multiflorum L.	LOLMG	italian rye-grass	Poaceae	23.3	95±5	95±5	21.6
Papaver rhoeas L.	PAPRH	field poppy	Papaveraceae	37.3	10±13	NA	0.9
Poa annua L.	POAAN	annual meadow grass	Poaceae	32.3	95±8	95±8	1.1
Sinapis arvensis L.	SINAR	charlock	Brassicaceae	29.2	50±17	90±11	4.3
Stellaria media (L.) Vill.	STEME	com. chickweed	Caryophyllaceae	36.0	38±42	83±10	27.9
Veronica persica L.	VERPE	com. field-speedwell	Scrophulariaceae	25.2	95±5	95±5	31.6
Viola arvensis Murray	VIOAR	field pansy	Violaceae	30.0	07±10	85±15	2.5

D, density of seeds per m² added on the experimental plots; **G**, mean percentage of seeds germinated in growth chambers; **V**, mean percentage of seeds with viable embryos; **R**, mean field emergence rate [calculated as the mean of the maximum densities of emerged seedlings during the first 8 month of the field experiment (September 2006-April 2007) *100 divided by the density of *viable* seeds sown].

The viability and germination ability of the sown seeds was determined by germination and dissection assays. 10 seeds of each species were kept in moist conditions in growth chambers, three replicates at 30°C/20°C day/night and three replicates at 20°C/10°C day/night temperature. Germinated seeds were counted and removed until germination ceased after approximately one month. Further germinations were provoked by a) drying the seeds for one week and re-humidifying them, b) stratifying the seeds for 3 weeks at 4°C and c) by twice adding a solution of gibberellins. Seeds not germinated after all these treatments (about 4 month in total) were dissected to count the number of viable embryos and to calculate the rate of viable seeds (Table 7).

C.II.2.2 Measurements

C.II.2.2.1 Plant densities

Weed plant densities were assessed approximately every month (except in winter) by determining and counting the number of plants of all species on three permanently installed metal frames of 0.36m² (0.6m*0.6m) per replicate plot (3*4 = 12 frames per treatment, * 9 treatments = 108 frames). As a control, additional frames were installed in the adjacent zone of each plot not sown with weeds (‘unsown zone f’, Fig. 10).

C.II.2.2.2 Biomass

Crop and weed aboveground biomass was assessed 5-6 times per year in 2007 and 2008 by manually cutting weed and crop shoots at 5cm from the soil surface on one non permanently installed quadrat of 0.36 m² per replicate plot (Fig. 10). Shoots were sorted to species, dried at 80°C for 48h, and weighted. These measurements were always done a few days prior to the cutting dates of the perennial crops, when crops and weeds had maximum biomass and impacts on the crop stand were minimal.

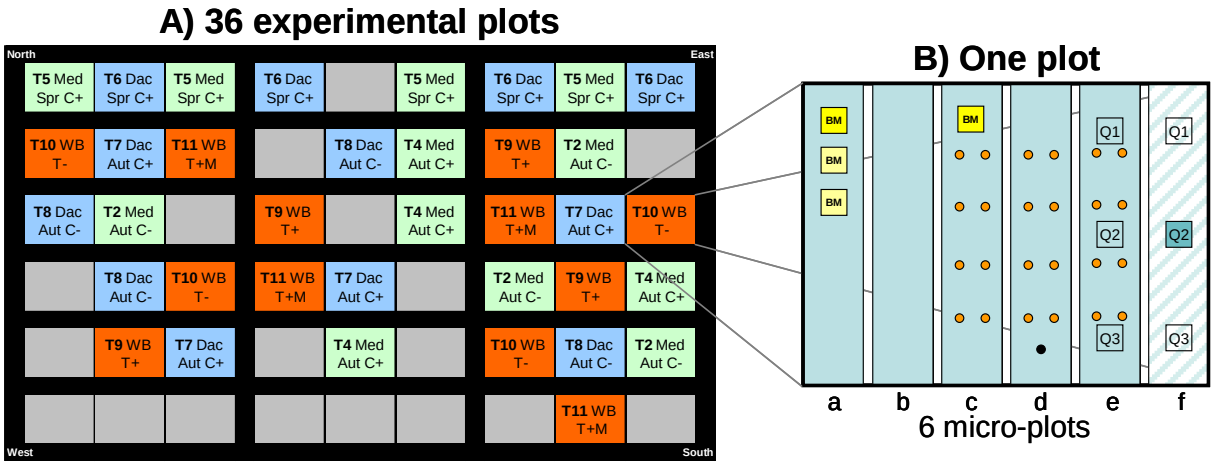

Fig. 10: **A)** Spatial set up of the 36 experimental plots (9 crop treatments * 4 repetitions) on an experimental field with 6*9=54 plots. **B)** Localisation of plant density and biomass measurements on the 6 micro-plots of each plot. Each plot measures 7.5 m x 10 m = 75 m². Black lines are 4 m wide alleys around the plots. Grey plots were not used. For practical reasons, both spring-sown crop treatments (T5 and T6) were grouped together (in the upper line of the graph). Each plot is composed by 6 micro-plots (a-f, about 1.5 m wide). On five micro-plots (a-e), weed seeds had been added to the soil (see section C.II.2.1.1), micro-plot f was the unsown control (striped). Quadrats (Q1-Q3) show the location of the fixed zones where weed plant densities were regularly measured; quadrats (BM) show the non-fixed zones, where the crop and weed biomasses were successively measured (destructive in the annual crops, 'quasi non-destructive' in the perennial crops due to hay cuttings few days later and regrowth); small red dots show the approximate location of the 8 soil cores taken for seed bank evaluation, the black dot the soil cores taken for chemical analysis.

C.II.2.2.3 Chemical soil parameters

Soil samples were taken 7 weeks after the beginning of the experiment and after two years at two soil layers (1: 0-30cm, 2: 30-60cm) using a '*Pürkhauer*' type soil core sampler (diameter = 5 cm) on micro-plots d (see details in Fig. 10). Chemical soil analyses of both sampling dates were performed by an external service '*Laboratoire Départemental de la Côte d'Or*' using standardized methods.

Results of the chemical soil analysis are summarized in Table 8. Both organic carbon and total nitrogen concentrations decreased always with soil depth. While carbon concentrations did not change from the first to the second sampling date, total nitrogen showed an increasing tendency which led to narrower C/N ratios.

Table 8: Organic carbon and total nitrogen concentrations in two soil layers 7 weeks after the beginning of the experiment and after two years.

Date	Soil horizon	n	Organic C [g/kg]	Total N [g/kg]	C/N	NO_3-N [mg/kg]	NH_4-N [mg/kg]
			Mean±SD	*Mean±SD*		*Mean*	*Mean*
18.10.2006	1 (0-30cm)	12	17.4±1.4	1.7±0.2	10.4	5.48	0.17
	2 (30-60cm)	12	13.0±2.4	1.3±0.3	9.9	7.98	0.47
12.11.2008	1 (0-30cm)	36	17.3±1.7	2.0±0.2	8.6	1.06	1.90
	2 (30-60cm)	36	11.0±1.6	1.4±0.2	8.2	0.80	1.27

Fig. 11 shows the spatial variation of the chemical soil parameters on the experimental field. Both organic carbon and total nitrogen concentrations were rather homogeneous but showed a weak gradient with slightly higher values on the plots on the southern part of the field (Fig. 11).

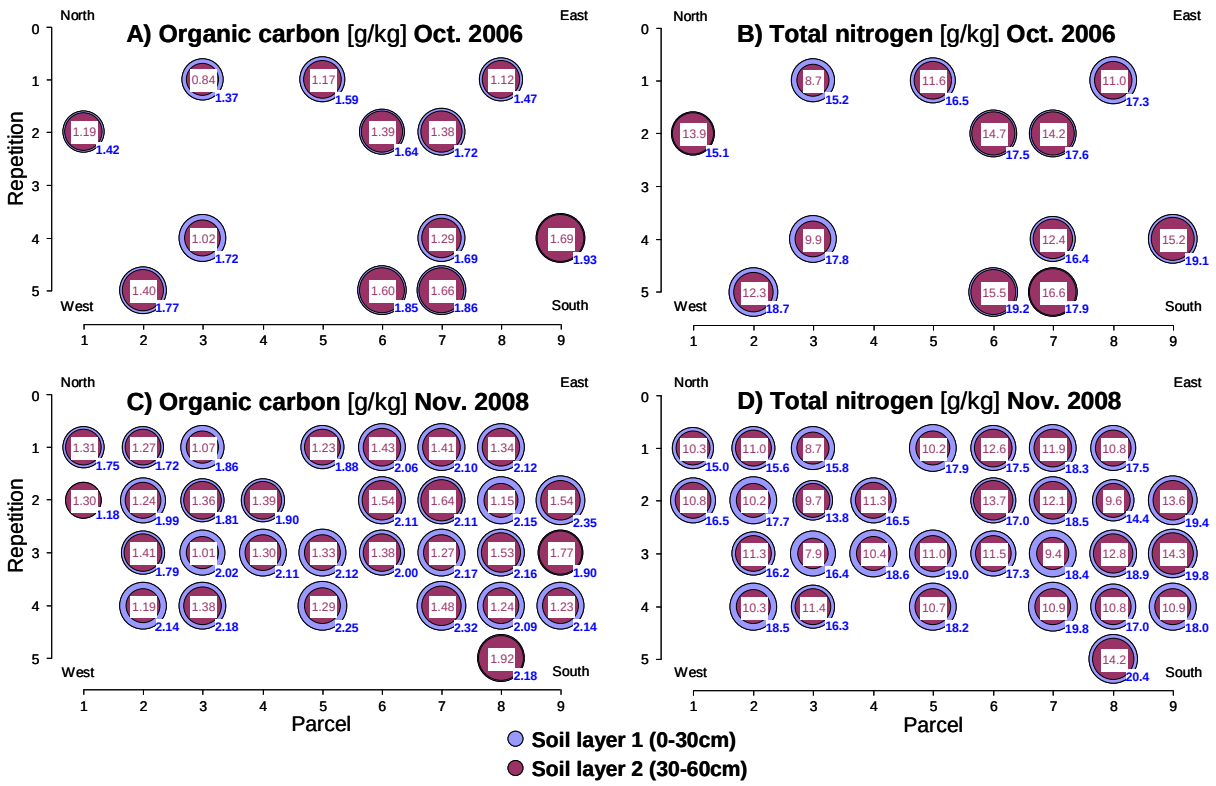

Fig. 11: Spatial heterogeneities of organic carbon and total nitrogen concentrations in the soil of the experimental field in October 2006 and November 2008.

The spatial arrangement (North-East-South-West) with 5 'Repetitions' and 9 'Parcels' corresponds to Fig. 10. The surface of the circles corresponds to the concentrations in g per kg of soil.

C.II.2.3 Statistical analysis

C.II.2.3.1 Emerged weed densities

The temporal development of weed species composition was compared between the nine crop treatments using Multiple Response Permutation Procedure (MRPP, McCune and Grace, 2002) with the Bray-Curtis distance measure, 5000 permutations and the recommended weighting factor $c = n/\sum(n)$ implemented in PC-ORD. Pairwise differences between all treatments were calculated for each observation date and the Bonferroni-corrected p-values were reported. Indicator Species Analysis (ISA, Dufrene and Legendre, 1997) with 5000 permutations implemented in PC-ORD 5 (McCune and Mefford, 1999) was used to calculate and test 'Indicator Values' (IV) for the emerged weed plants at the last observation date. The multivariate tests based on permutations of the group affiliations of the subjects (MRPP and ISA) are recommended for analyzing multivariate data containing many zeros and do not rely on assumptions about multivariate normality (Kenkel *et al.*, 2002; Sosnoskie *et al.*, 2006).

The effect of weed seed addition was assessed by calculating and plotting the differences between plant densities of adjacent sown and unsown plots (micro-plots e and f, Fig. 10) for each weed species at each observation date. Pairs of plots without any plants of the considered species (double zeros) were excluded.

C.II.3 Results

C.II.3.1 Dynamics of emerged weeds

C.II.3.1.1 Dynamics of weed plant density and diversity

In all three successions of annual crops, total weed plant densities showed strongly increasing tendencies during the 2.5 years experiment (starting at less than 10 plants/m² in 2006 and ending at about 200-800 plants/m² in spring 2009). In contrast, weed densities showed decreasing tendencies in all perennial crop treatments. Decreases tended to be stronger in *Dactylis* compared to *Medicago* crops. In spring 2009, weed densities averaged at 20-40 plants/m² in *Medicago* and 3-7 in *Dactylis* crops (see Fig. 12A and Fig. 13 for details).

The development of weed species richness showed a similar temporal pattern than weed abundances (increasing in annual crops, decreasing in perennial crops, *Dactylis* in particular, Fig. 12B). Moreover, spring-sown perennial crops had higher weed species numbers than the corresponding autumn-sown crops. However, changes in species numbers (Fig. 12B, linear scale) were much less pronounced than changes in weed densities (Fig. 12A, logarithmic scale). This resulted in strong changes of the ratio between weed species richness and weed plant density (Fig. 12C). This ratio decreased very quickly in all annual crops from 0.8-1 to 0-0.1 while it progressively increased in the perennial crop treatments, in particular in the *Dactylis* crops from 0.1 to about 0.7.

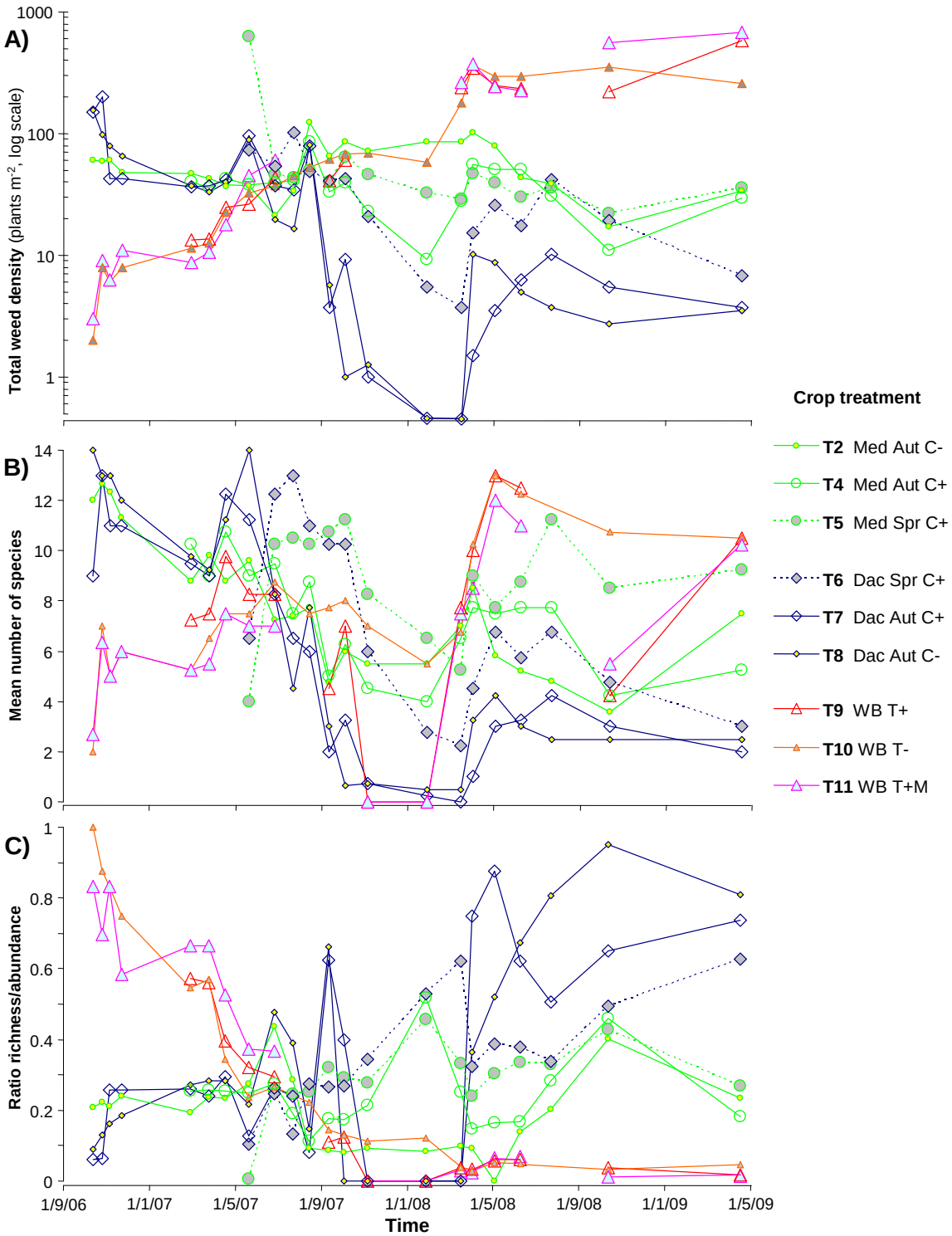

Fig. 12: Development of emerged weed densities (plants per m^2) (**A**), emerged weed species richnesses (**B**), and richness/abundance ratios (**C**) in nine crop treatments.

Med, *Medicago sativa* (green circles); Dac, *Dactylis glomerata* (blue rhombi); Aut, autumn sown perennial crops (continuous—traits); Spr, spring-sown perennial crops (broken----trait, symbols filled with grey); C+, 5 cuts/year; C-, 3 cuts/year (small symbols filled with yellow); WB, succession of annual crops (wheat-barley) (triangles); T+, with soil tillage after cereal harvest (red triangles); T-, without soil tillage after harvest (small orange triangles filled with grey); M, mustard intercrop (pink triangles filled with blue); see Table 6 for more details on the nine crop treatments.

C.II.3.1.2 Dynamics of weed community composition

After 2.5 years of contrasted crop management, the species composition of the emerged weed communities differed most strongly between all annual crop and all perennial crop treatments, as shown by the pairwise multivariate comparisons using the MRPP permutation technique (Table 9). The magnitude of the differences, indicated by the MRPP-A statistic ('within group agreement'), was strongest and always significant for all pairwise comparisons between annual crops and perennial cocksfoot crops (A-values varied between 0.48**** and 0.51****, see the first nine lines in Table 9). Pairwise differences between annual crops and perennial alfalfa crops were also highly significant and their magnitudes came at the second place (A varied between 0.36**** and 0.45****) followed by the differences between cocksfoot and alfalfa crops (A = 0.28**** - 0.41****, Table 9).

The differences between annual and perennial crops *increased* with time (see first 18 lines in Table 9). In contrast, differences between spring and autumn sown perennial crops were very strong during the first year (A = 0.27**** - 0.44****) and *decreased* with time. At the end of the experiment, differences between spring and autumn sown crops were lower than all other contrasts mentioned above, and only significant for alfalfa crops (A = 0.23****) but not for cocksfoot (A=0.05 ns). For alfalfa crops, weed communities differed significantly between the treatments with high and low cutting frequency at nearly all observation dates since these contrasted cutting treatments were set up in 2007. However, the amplitude of these differences were mostly weaker than the other differences mentioned above (A = 0.10** - 0.27****). In contrast, cutting frequency had no significant impact on species composition for cocksfoot crops at most observation dates (see Table 9 for details).

Table 9: Pairwise multivariate comparisons of emerged weed communities between 9 crop treatments for all survey dates during 2.5 years using the pairwise Multiple Response Permutation Procedure (MRPP). See Table 6 for details of the nine crop treatments (T2-T11). The table sows the MRPP-A values indicating the magnitude of the differences. They vary between 1 (no differences within the groups) and 0 (within groups heterogeneity equals the expectation by chance) (McCune and Grace, 2002). A-values >0.3 are shaded, cells are empty if the comparison is not available (insufficient data). P-values are Bonferroni-corrected (up to 36 comparisons per date); **** p<0.0001; *** p<0.0001; ** p<0.01; * p<0.05; ns, not significant (grey text).

Treatments compared				2006				2007										2008						2009
	Crop Sp.	Man.	Sowing	13-Oct	26-Oct	6-Nov	23-Nov	1-Mar	27-Mar	19-Apr	22-May	28-Jun	24-Jul	16-Aug	13-Sep	5-Oct	7-Nov	29-Jan	18-Mar	4-Apr	5-May	11-Jun	14-Oct	20-Apr
	Dac-ann							0.07ns	0.08ns	0.04ns	0.07ns	0.07ns			0.44****	0.47****	0.05ns	0.00ns	0.57****	0.55****	0.50****	0.34****	0.46****	0.51****
	Dac-ann										0.33****	0.24****			0.42****	0.45****	0.39**	0.24**	0.44****	0.40****	0.34****	0.26****	0.43****	0.50****
0	Dac-ann			0.17ns	0.23ns	0.16ns	0.12ns	0.16**	0.12*	0.11ns	0.10ns	0.00ns		0.18**	0.30****	0.37****	0.41****	0.46****	0.38****	0.54****	0.44****	0.42****	0.47****	0.50****
1	Dac-ann			0.00ns	0.21**	0.13*	0.08ns	0.15**	0.17***	0.12*	0.13**	0.04ns						0.51****	0.47****	0.51****	0.43****	0.40****	0.46****	0.50****
0	Dac-ann			0.53**	0.41**	0.43**	0.34**	0.22***	0.17***	0.23****	0.13*	0.06ns		0.09ns	0.32****	0.43****	0.41****	0.46****	0.30****	0.37****	0.36****	0.44****	0.52****	0.50****
	Dac-ann							0.12**	0.14***	0.07ns	0.10ns	0.13*			0.43****	0.58****	0.03ns	0.00ns	0.47****	0.41****	0.44****	0.36****	0.49****	0.50****
0	Dac-ann										0.31****	0.29****		0.35**	0.27****	0.34****	0.27****	0.30***	0.28****	0.40****	0.28****	0.34****	0.42****	0.49****
1	Dac-ann			0.40****	0.36****	0.35****	0.27***	0.21****	0.25****	0.22****	0.16***	0.11*						0.34****	0.40****	0.34****	0.37****	0.44****	0.50****	0.49****
1	Dac-ann										0.16***	0.27****						0.27***	0.36****	0.32****	0.24****	0.32****	0.43****	0.48****
	Med-ann										0.39****	0.36****			0.41****	0.40****	0.47***	0.40****	0.32****	0.27****	0.32****	0.23****	0.4****	0.45****
1	Med-ann							0.29****	0.31****	0.25****	0.17***	0.10*						0.37***	0.23****	0.21****	0.17****	0.15****	0.44****	0.44****
1	Med-ann										0.21****	0.33****						0.43****	0.30****	0.25****	0.25****	0.28****	0.41****	0.44****
0	Med-ann							0.30****	0.24****	0.28***	0.18***	0.09ns		0.28***	0.24****	0.32****	0.27****	0.26***	0.14**	0.23****	0.20****	0.21****	0.46****	0.43****
	Med-ann							0.19****	0.19***	0.12*	0.09ns	0.10ns			0.44****	0.46****	0.42**	0.34**	0.17***	0.20***	0.25****	0.14****	0.45****	0.43****
0	Med-ann										0.36****	0.35****		0.35****	0.25****	0.27****	0.24***	0.16**	0.19****	0.27****	0.24****	0.29****	0.37****	0.43****
1	Med-ann			0.16**	0.09ns	0.08ns	0.05ns	0.11*	0.09*	0.09*	0.07ns	0.08*						0.41****	0.21****	0.19****	0.25****	0.27****	0.49****	0.38****
	Med-ann							0.06ns	0.04ns	0.01ns	0.08ns	0.16***			0.15*	0.07ns	0.27**	0.37***	0.19***	0.23****	0.27****	0.25****	0.40****	0.38****
0	Med-ann			0.15*	0.03ns	0.03ns	0.05ns	0.11ns	0.05ns	0.07ns	0.06ns	0.04ns		0.05ns	0.07ns	0.03ns	0.02ns	0.00ns	0.06ns	0.14***	0.16****	0.28****	0.45****	0.36****
	Dac-Med	C-C+	Aut-Aut					0.04ns	0.03ns	0.02ns	0.11*	0.13*	0.26****	0.09*	0.23**	0.55****	0.37***	0.30**	0.34****	0.36****	0.21***	0.28****	0.12**	0.41****
	Dac-Med	C+	Aut-Aut					0.03ns	0.05ns	0.03ns	0.09ns	0.04ns	0.08ns	0.03ns	0.28****	0.33****	0.34***	0.32***	0.46****	0.51****	0.33****	0.20****	0.04ns	0.39****
	Dac-Med	C+	Spr-Aut								0.44****	0.39****	0.41****	0.35****	0.33****	0.28****	0.13*	0.08ns	0.27***	0.25****	0.15**	0.14**	0.10*	0.38****
	Dac-Med	C-C+	Spr-Aut								0.19***	0.41****	0.30****	0.25****	0.27****	0.32****	0.24***	0.24**	0.25***	0.21****	0.19***	0.16****	0.11***	0.36****
	Dac-Med	C-	Aut-Aut	0.09ns	0.14ns	0.11ns	0.13ns	0.03ns	0.03ns	0.02ns	0.09*	0.03ns	0.08*	0.04ns	0.12*	0.23**	0.26***	0.36***	0.27***	0.13**	0.13*	0.14***	0.05ns	0.35****
	Dac-Med	C-C+	Spr-Aut								0.43****	0.37****	0.44****	0.40****	0.40****	0.51****	0.44****	0.39****	0.22****	0.27****	0.19****	0.29****	0.24****	0.35****
	Dac-Med	C-C+	Aut-Aut	0.01ns	0.07ns	0.00ns	0.02ns	0.00ns	0.00ns	0.00ns	0.06ns	0.02ns	0.00ns	0.04ns	0.08ns	0.24****	0.25***	0.37****	0.37****	0.32****	0.25***	0.14****	0.05ns	0.33****
	Dac-Med	C+	Spr-Aut								0.43****	0.39****	0.36****	0.32****	0.36****	0.33****	0.38****	0.39****	0.31****	0.43****	0.23****	0.22****	0.10*	0.29****
	Dac-Med	C+	Spr-Spr								0.04ns	0.03ns	0.03ns	0.03ns	0.00ns	0.00ns	0.00ns	0.12*	0.09ns	0.13**	0.04ns	0.13**	0.00ns	0.28****
	Med-Med	C+	Spr-Aut								0.46****	0.43****	0.43****	0.40****	0.35****	0.26****	0.16**	0.07ns	0.16**	0.12**	0.14**	0.14**	0.12*	0.23****
	Med-Med	C-C+	Spr-Aut								0.23****	0.41****	0.32****	0.31****	0.26****	0.22****	0.23***	0.12ns	0.13**	0.13***	0.13**	0.12***	0.16****	0.15***
	Med-Med	C-C+	Aut-Aut					0.03ns	0.05ns	0.03ns	0.06ns	0.15***	0.13***	0.11**	0.19***	0.27****	0.22***	0.18**	0.14**	0.18****	0.11**	0.10**	0.06ns	0.13**
	Dac-Dac	C+	Spr-Aut								0.38****	0.37****	0.34****	0.27****	0.34****	0.33****	0.30***	0.21**	0.19**	0.18***	0.11*	0.07ns	0.07ns	0.05ns
	Dac-Dac	C-C+	Spr-Aut								0.38****	0.38****	0.38****	0.34****	0.35****	0.54****	0.36****	0.20**	0.10ns	0.13**	0.13**	0.13**	0.16***	0.04ns
	Dac-Dac	C-C+	Aut-Aut	0.15ns	0.13ns	0.09ns	0.10ns	0.00ns	0.00ns	0.01ns	0.00ns	0.06ns	0.08ns	0.05ns	0.02ns	0.34***	0.00ns	0.00ns	0.05ns	0.14**	0.03ns	0.02ns	0.08*	0.00ns
11	ann-ann		T+T-	0.02ns	0.02ns	0.03ns	0.13*	0.00ns	0.01ns	0.04ns	0.02ns	0.00ns						0.50****	0.02ns	0.03ns	0.03ns	0.03ns	0.44****	0.22****
0	ann-ann		T+T-					0.05ns	0.03ns	0.07ns	0.06ns	0.05ns			0.09ns	0.00ns	0.43***	0.46***	0.04ns	0.03ns	0.04ns	0.03ns	0.46****	0.20****
1	ann-ann		T+					0.04ns	0.08ns	0.04ns	0.02ns	0.04ns						0.04ns	0.01ns	0.04ns	0.05ns	0.05ns	0.29****	0.04ns

C.II.3.1.3 Dynamics of individual weed species

While total weed densities showed increasing tendencies in annual crops and decreasing in perennial crops, three groups of weed species can be distinguished by their reaction to the different crop treatments (see Fig. 13 for an analysis per treatment and Fig. 14 for an analysis per species). A **first group** of species showed increasing plant densities in all three annual crop treatments. This group included 10 species: *G. aparine, A. myosuroides, V. persica, S. arvensis, F. convolvulus, P. aviculare, P. persicaria & P. lapathifolium, A. arvensis,* and *P. rhoeas*. Some additional species showed increasing densities mainly in the annual crop treatment with OSFs (T10): *L. multiflorum, B. sterilis,* and *G. dissectum.* A **second group** of species showed high plant densities in the spring-sown perennial crops after sowing in 2007 including 12 species: *C. album, A. retroflexus, S. nigrum, S. asper, A. arvensis, C. bursa-pastoris, E. crus-galli, Senecio vulgaris, T. officinale, P. persicaria & P. lapathifolium* and *S. media*. However, the densities of these species decreased strongly with time. While some of them were no longer detected in both alfalfa and cocksfoot crops in 2008, others did not completely disappear (or reappeared for some periods, mostly with low densities in 2008), especially in spring-sown alfalfa. A **third group** of species emerged with high or medium densities after sowing of the autumn sown perennial crop treatments. Nearly all of them showed decreasing densities in most treatments, especially in cocksfoot regardless the cutting frequency (T7 and T8), while seven species did not completely disappear from the alfalfa treatments with a low cutting frequency (T2): *A. myosuroides, V. persica, B. sterilis, L. multiflorum, F. convolvulus, S. media, A. arvensis* and four species remained present in the alfalfa treatments with a high cutting frequency (T4): *V. persica, F. convolvulus, P. aviculare,* and *Sonchus sp.* Three species (*C. bursa pastoris, A. retroflexus,* and *V. arvensis*) showed strongly decreasing densities and were no longer detected at the end of the experiment in any of the four autumn sown perennial crops. *A. arvensis* was the only species that showed low but rather stable densities in all perennial crops. Finally, *G. dissectum* showed strongly decreasing densities in all perennial crops, but did not completely disappear after 2.5 years (Fig. 14).

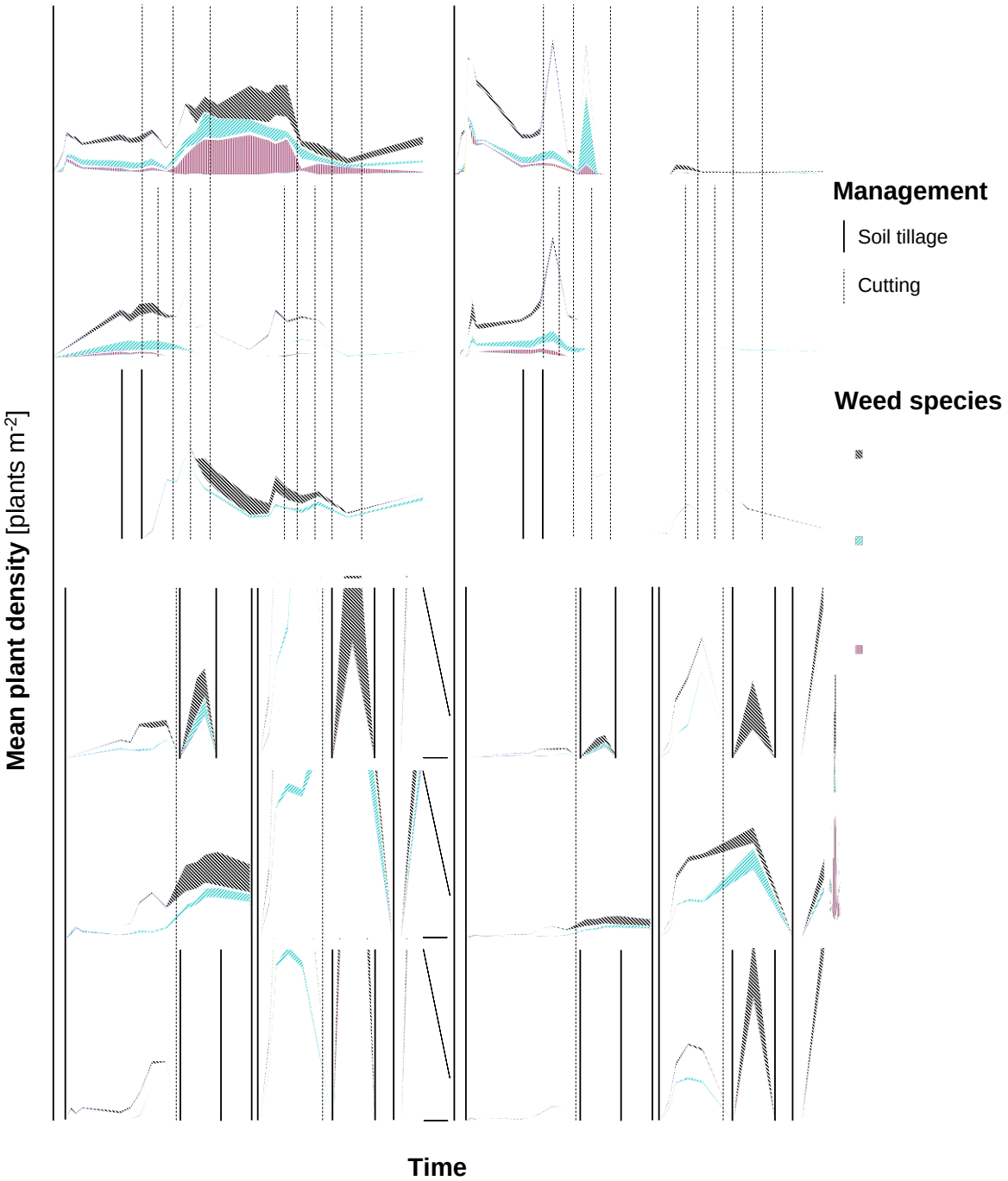

Fig. 13: Temporal development of emerged weed densities (plants per m^2) in six perennial crop treatments (T2-T8, upper part) and three successions of annual crops (T9-T11, lower part, plotted with two scales).

Bold vertical lines indicate the dates of soil tillage (all weed plants are destroyed, densities go back to zero); broken thin vertical lines indicate the cutting dates (weed plant densities do not go back to zero). Med, *Medicago sativa*; Dac, *Dactylis glomerata*; Aut, sown in autumn; Spr, sown in spring; C+, 5 cuts/year; C-, 3 cuts/year; WB, succession of annual crops (wheat-barley); T+/T-, with/without soil tillage after harvest; M, mustard intercrop; see Table 6 for more details on the nine crop treatments. The 21 most important weed species/genera are separated with a colour code, other minor species are grouped as 'other Grasses' and 'other Dicots'. Mean plant densities are linearly interpolated between successive measurements and soil tillage dates, real dynamics can differ due to plant emergences and mortality. Narrow peaks of plant densities (*e.g.* during 2007 in treatments T4, T7 and T8) indicate peaks of weed germination followed by high plant mortalities.

Time

Fig. 14: Temporal development of emerged plant densities of 19 major weed species in nine crop treatments. Scales of y-axes (plant densities) differ between the weed species, x-axes (time) have always the same scale. Mean plant densities (symbols) are interpolated between successive measurements with smooth lines, even if densities were temporally at zero due to soil tillage or cutting operations between successive measurements (compare to Fig. 13). Error bars represent standard deviations (N=12) that are not represented in Fig. 13.

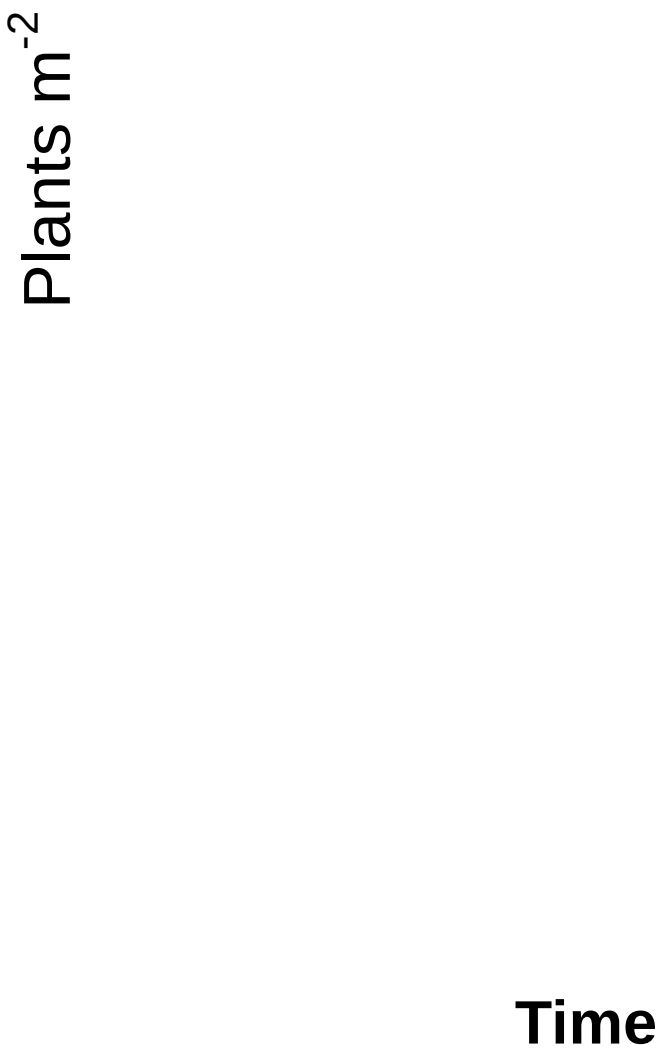

Fig. 14 (continued).

At the end of the experiment in spring 2009, the emerged weed communities were characterized by a number of indicator species for different crop treatments (Table 10). Ten weed species were significantly associated with one or several annual crop successions (T9-T11) and appeared only occasionally in the perennial crops. Six species were significantly associated with spring-sown alfalfa (T5) and one species (*T. officinale*) with both spring-sown perennial crops. Only one species (*S. media*) had an increased and nearly significant indicator value in autumn sown alfalfa (T2) while all other autumn sown perennial crop treatments had no significant indicator species. The ten indicator species of annual crops included the most abundant weed species, while most of the indicators for perennial crops were less abundant (see column 'Total abundance' in Table 10).

Table 10: Indicator Species Analysis of emerged weed communities in 9 crop treatments at the end of the experiment in spring 2009.

Species	Total freq. (1)	Total abund. (2)	Treatment (3)									T. IV_{max}	p-value	
			Alfalfa			Cocksfoot			Wheat-Barley					
			Aut.		Spring		Aut.		T+	T+ M	T-			
			C-	C+	C+	C+	C+	C-						
			T2	T4	T5	T6	T7	T8	T9	T11	T10			
	#	#	----------Indicator Values----------											
Indicators for autumn sown perennial crops														
Stellaria media	15	36	13	0	2	0	0	0	1	1	1	**T2**	0.0728	ns
Indicators for spring-sown perennial crops														
Poa annua	6	7	0	0	11	1	3	0	0	0	0		0.0326	*
C. album +polysp.	12	23	0	0	15	0	0	0	1	4	1		0.0322	*
Atriplex patula	4	22	0	0	18	0	0	0	0	0	0	**T5**	0.0022	**
Anagallis arvensis	41	109	1	4	**24**	1	0	0	2	4	3		0.0004	***
Capsella bursa-pastoris	6	7	1	0	**27**	0	0	0	0	0	0		0.0002	***
Sonchus asper +oleraceus	60	105	12	2	13	0	4	1	9	5	4		0.1082	ns
Taraxacum officinale	21	31	1	0	16	20	0	0	0	0	0	**T6**	0.0012	**
Indicators for annual crops														
P. pers. +lapathifolium	11	68	0	0	0	0	0	0	**29**	0	0		0.0026	**
Fallopia convolvulus	56	218	8	16	1	0	0	0	**31**	4	5		0.0002	***
Polygonum aviculare	41	151	0	15	0	0	0	0	**23**	2	15	**T9**	0.0038	**
Veronica persica	73	502	8	5	2	0	0	0	**27**	**22**	7		0.0016	**
Sinapis arvensis	42	1062	0	0	0	0	0	0	**45**	**38**	1		0.0002	***
Papaver rhoeas	16	33	0	0	0	0	0	0	3	**24**	9		0.0008	***
Galium aparine	59	3707	0	0	0	0	0	0	**36**	**50**	13	**T11**	0.0002	***
Alopecurus myosuroides	62	1347	1	0	0	0	0	0	**35**	**39**	22		0.0002	***
Lolium multiflorum	35	132	1	0	2	0	0	0	3	3	**54**	**T10**	0.0002	***
Bromus sterilis	23	119	1	0	0	0	0	0	0	0	**81**		0.0002	***

High Indicator Values (IV) are shaded in darker grey with three steps: IV≥10, IV≥20 and IV≥30.

(1) Total number of quadrats where the species is present (total = 152 quadrats, thus 16-18 quadrats/treatment).
(2) Total number of plants in all quadrats.
(3) See Table 1 for crop treatments T2-T11.

C.II.3.1.4 Effect of weed seed addition

During the first month of the experiment, field emergence rates were always much lower than the densities of viable seeds added to the soil at the beginning of the experiment. However, this ratio showed considerable differences between the weed species, separating three groups of species (Fig. 15). Field emergence densities were about 2-5 times lower than sowing densities for a first group of species including *G. aparine*, *V. persica*, *G. dissectum*, *S. media*, *A. myosuroides*, and *L. multiflorum*. For a second group including *C. bursa-pastoris*, *F. convolvulus*, and *B. sterilis*, emergence rates were about 10 times lower (thus 10-15% emergence). For a third group containing the remaining 8 sown species, only 1-5% of the sown viable seeds emerged during the 8 first month of the experiment (Fig. 15).

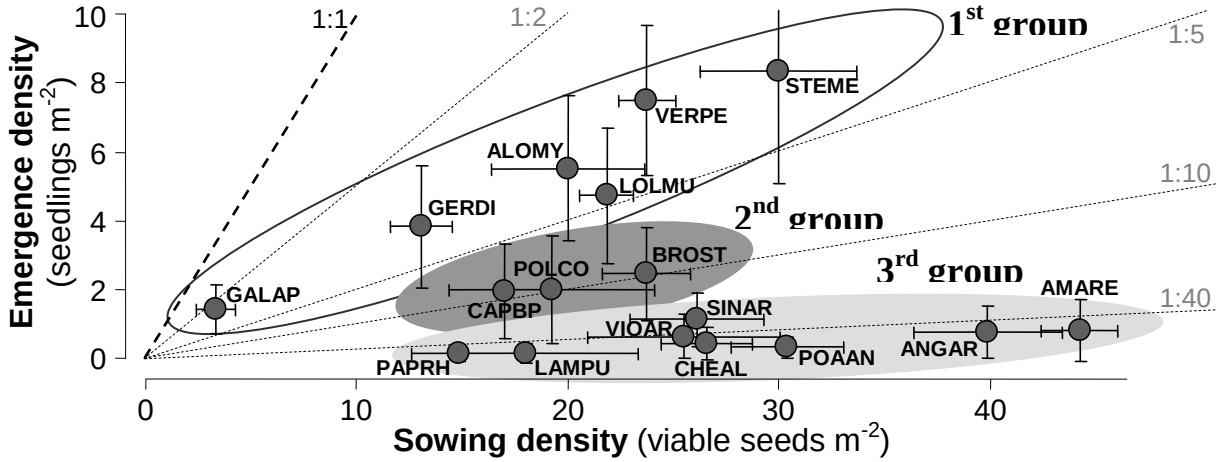

Fig. 15: Relation between weed sowing density and field emergence densities of 17 weed species.
See Table 7 for species codes. Field emergence are means (±SD) of maximum seedling densities on sown micro-plots during the first 8 month of the field experiment. SD of sowing density corresponds to the variability of seed viability tested in Petri dishes (cf. Table 7).

Comparisons of weed emergence densities on sown and unsown micro-plots showed that weed seed addition increased the plant densities of all sown weed species (except *C. bursa-pastoris*) during the first month of the experiment (Fig. 16). The initial positive effect of sowing increased with time for three species (group 1 in Fig. 16 including *A. myosuroides*, *B. sterilis*, and *G. aparine*, thus the species that showed strong population increases in the annual crops). The positive effect of seed addition remained more or less stable for four species (group 2 in Fig. 16 including *V. persica*, *S. arvensis*, *L. multiflorum and P. rhoeas*) and

decreased with time for eight species (group 3, see Fig. 16 for species names). For most species, the variances of the differences increased with time, probably reflecting the contrasted growth conditions in the nine crop treatments, which were pooled in the analysis shown in Fig. 16.

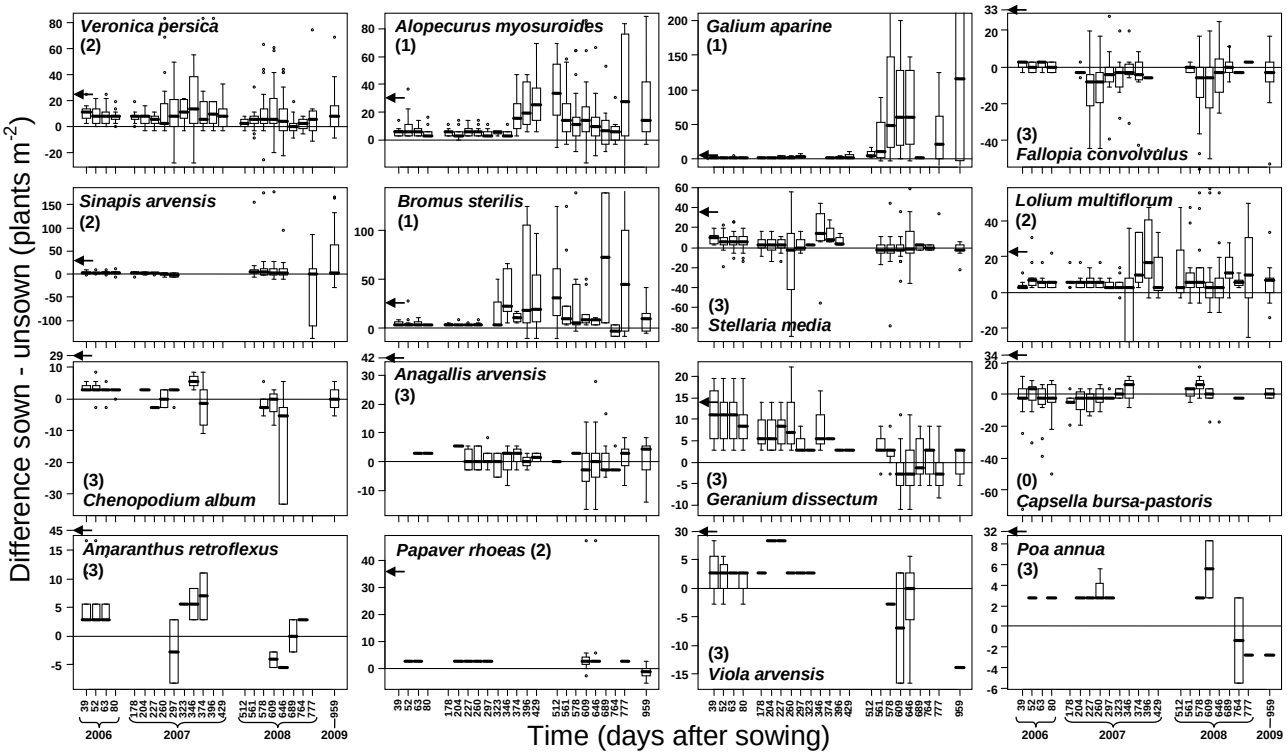

Fig. 16: Effect of weed seed addition on plant density of 16 weed species during the 2-years experiment.

The graphs show absolute differences of plant densities between adjacent sown and unsown plots; N varies between 15 and 24 for each date, double zeros are not plotted. Positive differences indicate that the sown plots had higher weed densities. Arrows (←) indicate the total density of seeds sown at the beginning of the experiment (Table 7). Species are sorted by their frequency of occurrence (*Veronica persica*, most frequent; *Poa annua*, least frequent, *Lamium purpureum* germinated only very rarely and is not shown).

C.II.3.1.5 Dynamics of weed and crop biomass

During the 2.5-years experiment, absolute and relative weed biomass decreased in the perennial crop treatments and increased in the annual crop treatments (Fig. 17 and Fig. 18). During the first month after perennial crop sowing (autumn 2006 or spring 2007), all 6

perennial crop treatments showed rather high weed biomasses (Fig. 18). For both spring-sown perennial crops and for the autumn sown cocksfoot crops, weed biomasses exceeded crop biomasses during the first months after crop sowing, while they were lower in both autumn sown alfalfa crops, which showed a quicker and more homogeneous initial crop establishment. After the first hay cutting, the proportion of weed biomass decreased strongly in nearly all perennial crop treatments. After 2-3 cutting operations, weeds accounted for no more than 1-20% of total biomass and decreased further to 0% in most treatments and replicate plots (Fig. 18). These decreases tended to be quicker (a) for all plots with the higher cutting frequency (5 cuts/year) and (b) in the three cocksfoot crop treatments, where weed biomass decreased often to 0% already during the first year (2007) and stayed that low until the end of the experiment. In contrast, substantial weed biomasses re-appeared in some alfalfa plots during the second year (2008), especially in those with the low cutting frequency (3 cuts/year).

In general, all weed species showed a higher mortality and a much weaker regrowth capacity after cuttings than both perennial crop species. However, the biomass of broad-leafed weeds often decreased more quickly than the biomass of grasses. Until the first cut in 2008, grasses (mainly *B. sterilis* and *A. myosuroides*) accounted for 20 to 60% of the biomass in alfalfa with a low cutting frequency. Most of these grass plants germinated already in autumn 2007, survived the winter but disappeared at the first cutting in 2008. This ‘problem’ did not appear in any cocksfoot crop treatment nor in the spring and autumn sown alfalfa with the higher cutting frequency, where weed densities accounted for only 0-15% of the total biomass in 2008 and decreased further with time (Fig. 18).

While all perennial crops showed decreasing weed biomass during the experiment, the opposite was true for annual crops, where broad-leaved weed species including *Galium aparine*, *Polygonum sp*., and *Sinapis arvensis* as well as grasses such as *A. myosuroides* showed increasing biomass during the two years (Fig. 17, Fig. 18). In the first year (2007), most of the winter wheat plots showed much lower weed biomasses than the perennial crops, weeds accounted for 0-20% of total biomass. This proportion was much higher in 2008, where mainly dicotyledonous weeds accounted for up to 40% of the total aboveground biomass (Fig. 17, Fig. 18).

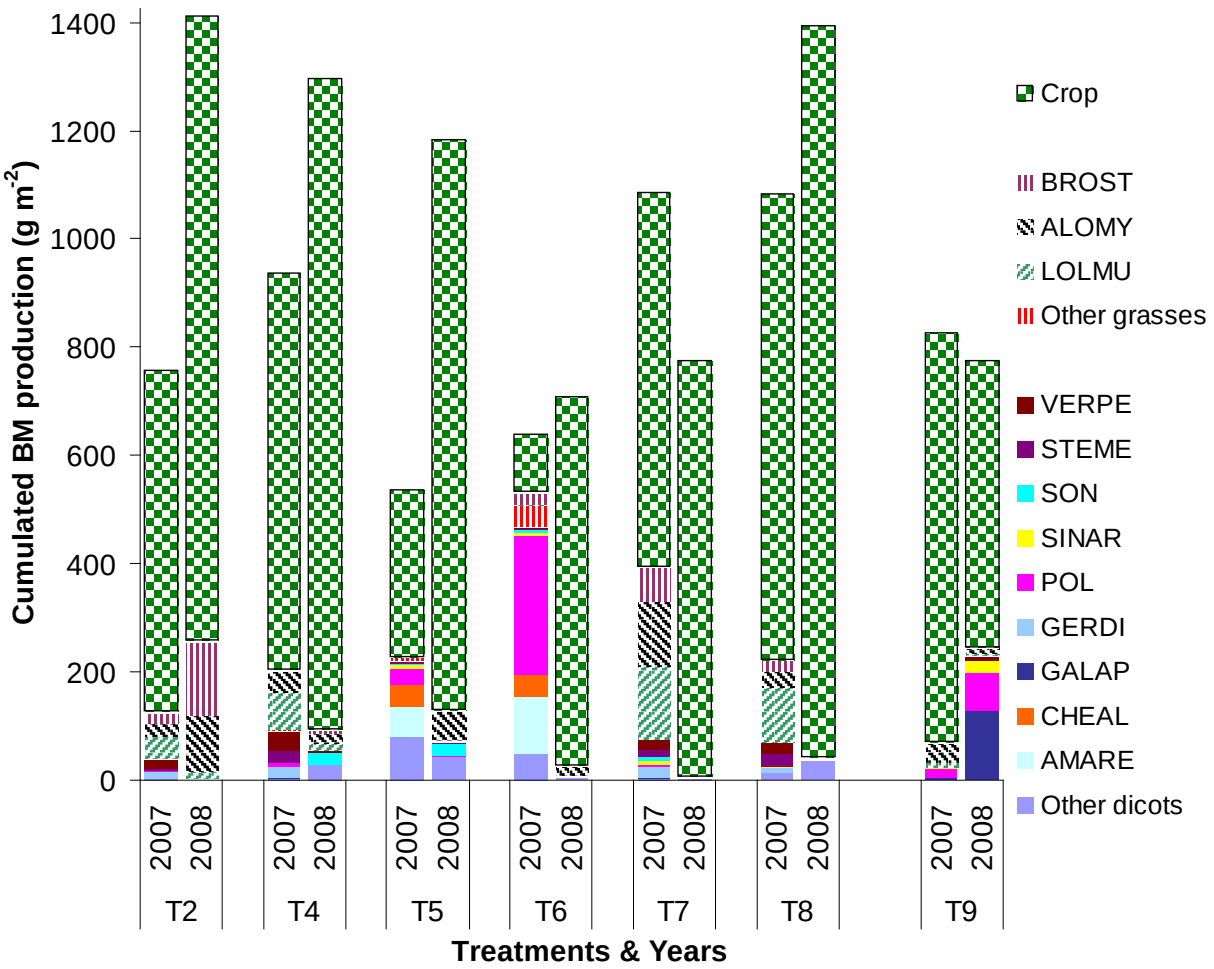

Fig. 17: Cumulated crop and weed biomass production in 2007 and 2008 in different crop treatments. T2-T5, perennial alfalfa crop; T6-T8, perennial cocksfoot crop; T9, annual cereal crops (winter wheat in 2006-2007, spring barley in 2008). See Table 6 for details on the crop treatments. Weed biomass is separated to grasses (striped, above) and dicotyledonous species (not striped, below), 12 important weed species/genera are separated with a colour code, all other species with lower biomasses are grouped as 'other Grasses' and 'other Dicots'.

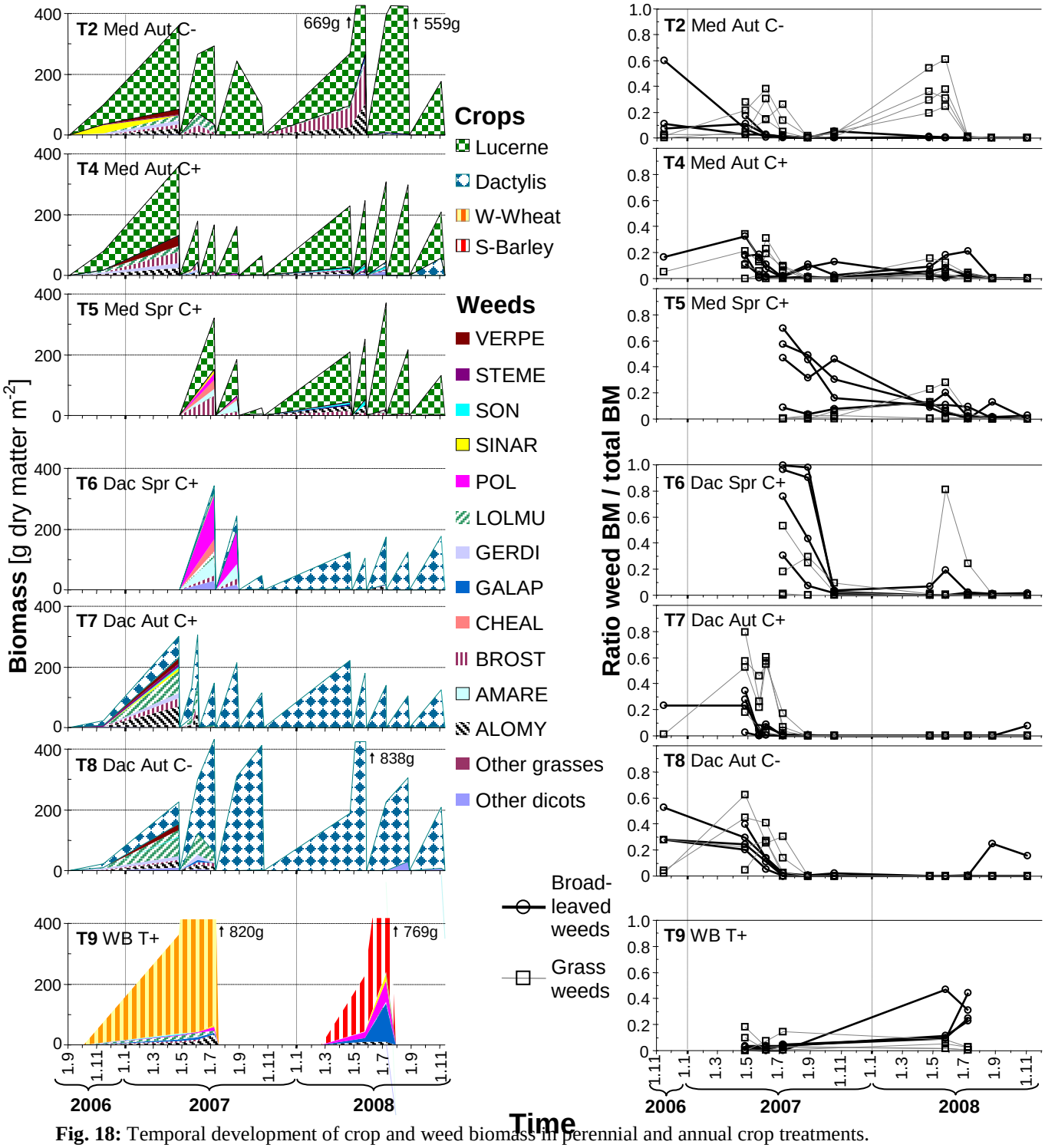

Fig. 18: Temporal development of crop and weed biomass in perennial and annual crop treatments.

Left part: Mean absolute biomasses of crops and weeds (g dry matter above 5 cm from the soil surface per m², N=4). Cumulated values higher than the plotted limit (400g/m²) are given as numbers. Biomasses go down to zero at crop cutting harvesting dates. Successive measurements are linearly interpolated; however, real biomass dynamics may differ. **Right part:** Relative biomass of grass (□ quadrats) and broad -leaved (○ circles) weeds expressed as the ratio of weed biomass on total (crop + weed) biomass. Each point linked by traits represents one replicate block. Med, *Medicago sativa*; Dac, *Dactylis glomerata*; Aut, autumn sown; Spr, spring sown; C+, 5 cuts/year; C-, 3 cuts/year (see Table 6B or Fig. 16 for cutting dates); WB T+, succession of annual crops with soil

tillage after harvest (T9). The two other annual crop treatments (T10, T11) had similar crop and weed biomasses and are not shown. Dotted vertical lines indicate the 1st January of each year (for orientation purposes).

Comparisons of crop and weed biomasses for each replicate plot at each measurement date showed contrasting patterns. Negative relationships were observed for all five measurement dates in 2007, *i.e.* plots with high crop biomass had low weed biomass and *vice versa* (Fig. 19A). These relations followed negative exponential or power laws. For each successive measurement, regression lines moved closer to the axis, *i.e.* the weed biomasses strongly decreased with time during 2007. In contrast, crop and weed biomass did not show any negative relations in 2008 (Fig. 19B). A majority of plots did not contain any weed biomass at all measurement dates in 2008 (as for the last measurement in 2007), some plots combined high crop and weed biomass at two dates in 2008 leading to slightly positive relations (Fig. 19B). These cases corresponded mainly to the annual crop treatments (spring barley) and to the autumn sown alfalfa crops with a low cutting frequency (see T2 in Fig. 18). However, total weed biomass was mostly lower than crop biomass (Fig. 19B).

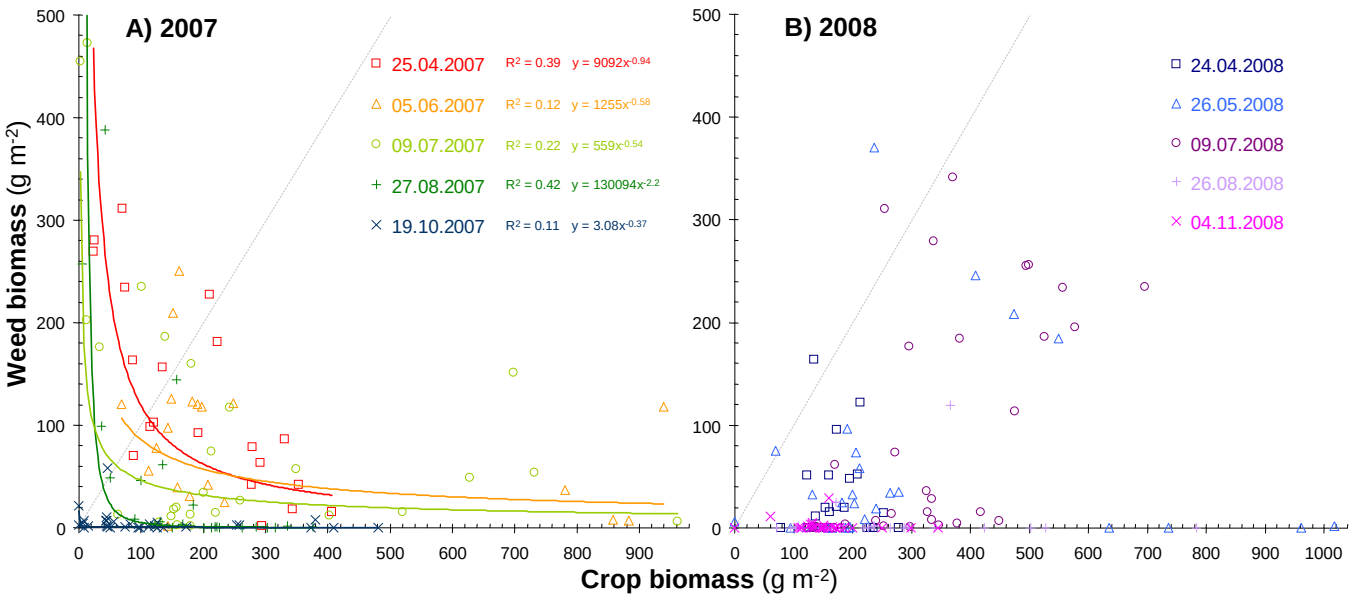

Fig. 19: Relation between crop and weed biomass at five observation dates in 2007 (**A**) and 2008 (**B**). Each symbol corresponds to one replicate plot at one sampling date. The nine crop treatments are not distinguished. Continuous coloured lines show power regressions for each date in 2007. Broken grey lines show equal crop and weed biomasses.

C.II.4 Discussion

C.II.4.1 Differences between crop treatments

Results of this 2.5-year field experiment show that weed populations reacted in contrasted ways to the compared crop treatments. At the end, differences in weed plant densities, diversities, biomasses and species composition were strongest between the annual and perennial crops (*cf.* summary in Table 11). Differences between autumn and spring-sown perennial crops and between annual crops with or without soil tillage after harvest came at the second and third places, while the other factors (forage crop species, cutting frequency and the mustard intercrop) resulted in lower differences (Table 11).

Table 11: Summary of results for five crop treatment comparisons (detailed in previous Figures and Tables).

Criteria	Time	Treatment comparison				
		Crop type	**Species**	**Sowing season**	**Cutting frequency**	**Tillage in intercrop**
		Annual *vs.* **P**erennial	**D***actylis vs.* **M***edicago*	**S**pring *vs.* **A**utumn	3 *vs.* 5/year	With *vs.* without
Emerged weed plants						
Density (Fig. 12A, Fig. 13)	Beginning	P >> An	=	=	=	=
	End	**An >> P**	**M > D**	**D: A > S**	=	**T+ >~ T-**
Diversity (Fig. 12B)	Beginning	P >> An	=	S > A	=	=
	End	**An >> P**	**M >> D**	**S > A**	**C- >~ C+**	=
Ratio richness/abundance (Fig. 12C)	Beginning	An >> P	=	A >~ S	=	=
	End	**P >> An**	**D > M**	=	=	=
Biomass (Fig. 17)	Beginning	P > An	D > M	S >> A	=	=
	End	**An >> P**	=	=	=	=
Species composition (Table 9)	Beginning	≠ ≠	=	≠ ≠	=	=
	End	≠ ≠ ≠	≠ ≠	≠	**M:** ≠	≠

End; last months of the experiment; Beginning; first months of the experiment; An, Succession of annual crops; P, Perennial crops; D, *Dactylis glomerata*; M, *Medicago sativa*; S, Spring-sown; A, Autumn sown perennial crops; C-, cut 3 times per year; C+, 5 cuts/year; T-, without soil tillage during intercrops; T+, with soil tillage; >>, much higher than (white cells); >, higher than (light grey cells); >~, tends to be higher than (grey cells); *S:* / *D:*, differences exist only for Spring-sown / *Dactylis* crops; ≠ ≠ ≠, very strong differences (white); ≠ ≠, strong differences (light grey); ≠, medium differences (grey); =, no differences (black).

Table 12: Factors differing between five crop treatment comparisons (as in).

Factor	Treatment comparison				
	Crop type	**Species**	**Sowing season**	**Cutting frequency**	**Tillage in intercrop**
Soil disturbance (superficial tillage, sowing)*	An >> P	D >~ M (roots?)	Season	=	T+ > T-
Aboveground vegetation disturbance (hay cuttings /crop harvesting)*	P > An	=	A >~ Sp	C+ >> C-	T+ >~ T-
Fertilisation (N-fertilizer *vs.* N-fixation)	≠	≠	=	=	=
Vegetation cover (competition for light)*	≠ ≠ growth dynamics	≠ growth dynamics	≠ ≠ crop establishm.	C- > C+	=
Allelopathy	??	??	=	=	=

* Impacts of these factors on the weed life cycle are detailed in Table 13.

C.II.4.1.1 Plant densities

Emerged plant densities and biomasses of many common annual weed species showed stable or decreasing tendencies in all perennial crop treatments. Such weed population dynamics may be surprising given the complete absence of soil tillage and specific weed control techniques in the PFCs. (Possible mechanisms of these declines will be discussed below). Interestingly, reductions in weed abundances in PFCs were much more pronounced than reductions in species richness leading to improved diversity/density-ratios (Fig. 12) that may be useful for reducing the 'weeds trade-off' (see § A.III.3 in the general introduction).

In contrast, some weed species showed strongly *increasing* population sizes in the succession of annual crops, as indicated by the increasing field emergence densities (Table 10, Fig. 12, Fig. 13) and weed biomasses (Fig. 17) during the 2.5 years experiment compared to the perennial crops. These strong weed increases in the annual crops are probably due to events of weed seed multiplication during the experimental period. It can not be explained by dense background seed densities or the initial weed seed addition, which would be visible in all treatments of the randomized block experiment, which was not the case for any of the 16 sown species. In both spring-sown perennial crops, considerable weed seed production occurred probably during the first month after crop sowing due to the slow initial crop establishment and the late first cutting (see discussion on the mechanism below).

C.II.4.1.2 Species composition

Due to these heterogeneous weed population dynamics, species composition varied most strongly between annual and perennial crops at the end of the experiment, (Table 9). After the

succession of annual crops, plant communities were characterized by several common annual weed species including those often reported as problematic in annual cereal crops such as *G. aparine*, *A. myosuroides*, *F. convolvulus*, *P. aviculare*, *P. rhoeas*, and *Sinapis arvensis*.

C.II.4.2 Grassland management practices

While crop management options could not be distinguished in the large-scale weed surveys, the field experiment permitted to compare tree treatment factors that were partially crossed: two different perennial crop species, two sowing seasons and two cutting frequencies. Such comparisons were rarely done in the previously published studies (reviewed in Article 1, Meiss *et al.*, 2010a). Weeds reacted differently to these treatments, which will be discussed in the following. These differences may give first indications on the optimal perennial crop management and may inform about the mechanisms potentially underlying the impacts. However, one should keep in mind that the differences between these treatments were mostly much less strong than between annual and perennial crops (see overview in Table 11).

C.II.4.2.1 Sowing date

Among the three treatment factors, crop sowing date (autumn *vs.* spring) had strongest impacts on weed species composition, while the total weed densities were rather similar. In the emerged weed vegetation, the differences in species composition decreased with time (Table 9). These results highlight the importance of the establishment phase of the perennial crop. Sowing date is known to have strong impacts on weed species composition in annual crops (Hald, 1999), but such impacts have never been demonstrated for perennial crops.

C.II.4.2.2 Crop species

Although legume (*Medicago sativa*) and grass (*Dactylis glomerata*) crops may differ in various aspects including temporal growth dynamics, nitrogen fixation and fertilisation regimes, competitive ability and allelopathy (Table 12), crop species was not the most important treatment factor in the field experiment (see overview in Table 11). This is in line with previous studies by Andersson and Milberg (1996; , 1998), who detected strong differences in weed density and species composition between annual and perennial ley crops during 6-year crop rotations, but not between grass and grass-legume leys. Similarly, Bellinder *et al.* (2004), did not find differences in weed seed banks after alfalfa and clover forage crops.

However, some differences in density and diversity of the emerged weed vegetation were detected. During the establishment phase, cocksfoot crops showed higher weed densities and biomasses than alfalfa, which might be due to reduced competition. In contrast, cocksfoot crops had even lower weed densities and diversities than alfalfa during the second half of the experiment, which might be due to reduced weed emergence (see chapter D.II 'Underlying mechanisms' below).

C.II.4.2.3 Cutting frequency

Hay cuttings are often the only mechanical disturbances in PFCs and might have strong direct and indirect impacts on weeds (destroying weed shoots and modifying the competitive environment). It might thus be surprising that the difference between the high and the low cutting frequency (5 *vs.* 3 cuts per year) had only rather low impacts in the field experiment. These low differences are in contrast to the high differences between annual and perennial crops that also differed by the cutting frequency (annual cereal crops were harvested only once per year).

The lower cutting frequency led to slightly increased final weed species diversities. This may indicate that the lower cutting frequency allowed a higher number of different species to successfully terminate their life cycles. In contrast, no significant effects could be detected on final plant *densities*, although plots with the lower cutting frequency showed higher weed biomass at some measurement dates. Two antagonistic processes might have caused this balanced result: the lower cutting frequency might have reduced the direct destruction of weed shoots but also lead to longer periods where the soil is covered by the crop canopy increasing competition for light. The latter mechanism was visible in cocksfoot, where the lower cutting frequency led even to higher cumulated crop biomass production (Fig. 17). This was also observed in other studies. Bell et al. (1989) showed that yield and competitive ability of *Bromus willdenowii*-grasslands in New Zealand increased when cutting frequency was reduced (40-50 days instead of 10, 20, or 30 days). In a similar way, Hoveland et al. (1996) reported that *Medicago sativa* grasslands in Georgia, USA, showed better regrowth with a 4 or 6 weeks interval compared to 2 weeks, where yields were reduced by 50% and weed invasion favoured.

C.II.4.3 Underlying mechanisms

Decreasing weed population dynamics in PFCs may be quite astonishing, given the complete absence of herbicides and soil tillage and the sowing of 17 weed species at the beginning of the experiment. Other mechanisms must thus be responsible for these reductions.

Annual and perennial crops differ in several aspects that may affect the growth of weeds (*cf.* Table 4 in the general introduction). Thanks to the rather complex study design comparing nine crop treatments and the high temporal resolution of weed density and biomass observations, this experimental study allows to learn more about several of the mechanisms potentially underlying the impacts of PFCs on weeds. This has, to our knowledge, rarely been investigated previously. In the following three paragraphs (C.II.4.3.1-3), I will discuss three main factors governing the impacts of PFCs on arable weeds: the absence of **soil tillage (A)**, the strong and temporally extended **competition (B)**, and the frequent **hay cuttings (C)**. Table 12 gives an overview how these factors varied with the experimental treatments. Our results suggest that these three factors affected several important parts of the weed life cycle (Fig. 20). These impacts are also summarized in Table 13.

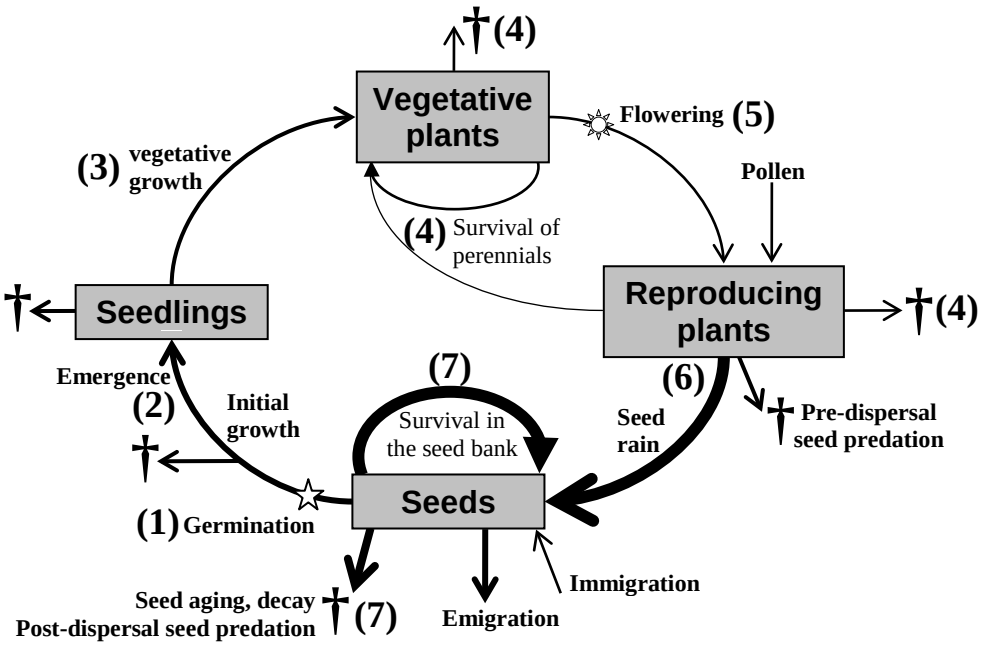

Fig. 20: Life cycle of annual and perennial weeds.

Grey boxes, four stages; arrows, transitions between stages; **†,** mortality. The thickness of the arrows corresponds to approximate densities of individuals (varies between species and populations). The survival of established plants (4) will be more important for perennial species, seed rain and the survival of seeds in the seed bank will be more important for annual species. The numbers (1-6) corresponds to the weed life stages in Table 13 showing the possible impacts of PFCs.

Table 13: Mechanisms causing the impacts of perennial forage crops (PFCs) on weeds.

Hypothetic impacts of three characteristics of PFCs (A, B, C) on seven stages of the weed life cycle (1-7, corresponding to Fig. 20).

<table>
<tr><th rowspan="2">Weed life cycle stage</th><th colspan="4">Characteristics of PFCs</th></tr>
<tr><th colspan="2">A) Absence of soil tillage</th><th>B) Temporally extended vegetation cover</th><th colspan="2">C) Frequent hay cuttings</th></tr>
<tr><td>(1) Germination</td><td>Reduce*** (M3) (lack of stimulation by light or oxygen, lack of soil contact, no seeds digged up?)</td><td>or increase^{0} (M3) (seeds not deeply buried?)</td><td>Reduce* (M3) (less light quantity and modified light quality under plant canopy?)</td><td colspan="2">*Increase*^{0} (M3) (temporarily reduced vegetation cover -> more light on soil surface?)</td></tr>
<tr><td>(2) Emergence</td><td colspan="2" rowspan="5">Increase*** (M3) (reduced plant destruction)</td><td rowspan="5">Reduce*** (M3, M5) (competition for light, water and nutrients)</td><td>/</td><td rowspan="3">or increase^{0} (temporarily reduced competition for light?, M3, A5)</td></tr>
<tr><td>(3) Vegetative growth</td><td rowspan="3">Reduce*** (increased shoot destruction, M3, A4, A5)</td></tr>
<tr><td>(4) Plant survival</td></tr>
<tr><td>(5) Flowering</td><td>/</td></tr>
<tr><td>(6) Seed production</td><td>/</td></tr>
<tr><td>(7) Seed survival</td><td colspan="2">Reduce* (seeds stay on surface: more seed predation A6-8, higher mortality, more fatal germinations?)</td><td>Reduce** (better habitat for seed predators, A8)</td><td colspan="2">*Increase** (reduced seed predation due to habitat modification or predator destruction, A8)</td></tr>
</table>

*** high evidence; ** medium evidence; * low evidence; ^{0} no evidence; / probably no strong impacts; M3 Manuscript 3, A8 Article 8, etc.

C.II.4.3.1 Soil tillage (A)

Soil tillage is known to be one of the most important crop management techniques determining weed population dynamics and community composition in arable fields (Kegode *et al.*, 1999; Barberi and Lo Cascio, 2001; Menalled *et al.*, 2001; Davis *et al.*, 2005; Murphy *et al.*, 2006). In our experiment, the observed differences in weed population dynamics between (i) annual and perennial crops, (ii) spring and autumn sown perennial crops and (iii) the different intercrop treatments of the annual crops were probably caused in large parts by differences in soil tillage (see Table 12 for an overview).

The experimental results give evidence for two major and well-known impacts of soil tillage on weeds: (1) the mechanical destruction of established weed plants and (2) the stimulation of new weed emergence. The first mechanism has mainly negative effects on weed population dynamics (and is therefore widely used in various forms of mechanical weed control). However, in destroying weed (and crop) plants, soil tillage and other mechanical disturbances may also create a less competitive environment that may be beneficial for other weeds (see

discussion on interactions between competition and (aboveground) disturbances below). The second impact (stimulation of weed seed germination by soil tillage), may have positive or negative effects on weed populations depending on the reproductive success of the germinating seeds. Both impacts may occur simultaneously making the analysis rather difficult. Moreover, different weed species might react differently according to their traits.

Previously published experimental results (Sjursen, 2001; Albrecht, 2005; Hiltbrunner *et al.*, 2008) as well as the large-scale weed surveys (chapter C.I) suggest that biennial and perennial plant species are less well adapted to regular soil tillage than annual species, which is in line with ecological succession theory. However, the present experiment was mainly concentrated on annual weed species (that were sown on all plots at the beginning), while frequencies of naturally occurring perennial weeds were mostly too low to see any significant differences. Only *Taraxacum officinale* showed slightly increasing plant densities in some spring-sown perennial crops (Fig. 14), which had, however, no detectable effects on weed biomass.

Perennial and annual crops differed by several tillage operations per year. The first differential soil tillage took place only four weeks after the establishment of the experiment when the sowing of winter wheat was prepared of the plots of the annual crops. This event was probably the main cause of the lower weed densities and biomasses in winter wheat compared to most plots of the autumn-sown perennial crops until spring 2007 (Fig. 13, Fig. 18) due to the two mechanisms cited above. First, this supplementary tillage operation probably destroyed the big number of weed seedlings that germinated after the initial soil tillage four weeks ago. This corresponds to the well known ‘false-seed-bed technique’ that is used especially in IWM and organic farming systems for depleting the superficial weed seed banks before crop sowing (Rasmussen, 2004; Chikowo *et al.*, 2009). Second, weed seed emergence after this second tillage operation in October 2006 was much lower than four weeks earlier (due to modified climatic conditions or weed seed dormancy). It is well known that the delaying of crop sowing in autumn may considerably reduce the weed infestation in annual cereal crops (Rasmussen, 2004). Both the false seed bad technique and delayed sowing dates are often recommended for IWM in annual crops and might also be beneficial for reducing weed pressures during the establishment phase of perennial crops.

In the annual crops, established weed plants were also mechanically destroyed by soil tillage during the intercrop periods after cereal harvest in late summer and autumn/winter of both

2007 and 2008, while big numbers of weed plants of various species survived in the OSFs resulting in higher weed plant densities (Fig. 13) and biomasses (Fig. 18) in this treatment.

However, all perennial crop treatments, which were not tilled during the whole experiment, had considerably *lower* final weed densities than all annual crop treatments. Other processes with compensating effects on weed population dynamics must thus have taken place. Empirical evidence for the lack of stimulation for weed germination will be discussed in the following. Other compensating effects may be linked to the fact that more weed seeds stayed on the untilled soil surface of PFCs. This might result in reduced seed dormancy and increased numbers of (fatal) germinations (Benvenuti *et al.*, 2001), increased seed decay by micro-organisms (Wagner and Mitschunas, 2008) or increased seed predation rates (which will be analyzed in Chapter C.IV).

While the destruction of established weed plants was obvious for several soil tillage events, there are also strong indications that tillage favoured the germination and establishment of new weed plants. First, strong weed emergences were observed after most soil tillage periods except in winter (Fig. 13). As expected, the species composition that emerged after the tillage events varied strongly according to the tillage period. The soil tillage in April 2007 (applied for seed bed preparation of the spring-sown perennial crops) had stimulating effects on several spring and summer emerging weed species including *C. bursa-pastoris*, *Chenopodium album*, *Amaranthus retroflexus*, *Echinochloa crus-galli*, *Polygonum lapathifolium*, and *P. persicaria*. In contrast, these species were absent form all other treatments that were not tilled in this season.

After the first month of the experiment, the perennial crops often showed much lower weed emergence rates compared to the annual crops. This is another strong indicator for the importance of soil tillage for weed recruitment. In this way, soil tillage in February 2008 and 2009 (seedbed preparation for the annual crops) stimulated the emergence of weed species that are known to emerge preferentially in winter and early spring (*G. aparine*, *A. myosuroides*, *Polygonum sp.*, *S. arvensis*, and *V. persica*), while the soil tillages after cereal harvest in August 2007 and August 2009 stimulated the emergence of species including *A. retroflexus*, *L. multiflorum*, *A. myosuroides*, *G. aparine*, *S. arvensis* (Fig. 13) that are typical for summer or autumn sown crops.

The last indication for a strong impact of the lack of soil disturbance in perennial crops is the reduced weed emergence compared to the regularly tilled annual crops. Among the perennial

crop treatments, weed emergence was even more reduced in the *Dactylis* crops even if this crop showed higher initial weed densities and higher seed production. In this crop, the soil surface was generally harder and often intertwined with fine and dense grass roots, while the soil surface in the *Medicago* crops was looser and often wetter, and comprised less superficial roots (*Medicago* roots are known to grow deeper than *Dactylis* grass roots), which might have favoured weed germinations.

C.II.4.3.2 Competition (B)

Competition for common growth resources (light, water, nutrients) and space is probably the most important direct interaction between crops and weeds. An established and dense plant canopy can affect several important stages of the weed life cycle (see Fig. 20 and Table 13 for an overview). Germination rates may be reduced due to a lack of light stimuli and a modified light quality under the canopy (Huarte and Arnold, 2003). Initial seedlings growth may be affected due to a reduced availability of water and nutrients or allelopathic interactions (Xuan and Tsuzuki, 2002). After seedling emergence, competition (for light) is probably the most important factor determining weed growth, biomass and seed production in arable fields of temperate cropping systems. There are several indications that competitive interactions played an important role for weed (and crop) growth in our experiment:

- When pooling all crop treatments, crop and weed biomass showed strong negative correlations for all measurement dates during the first year of the experiment suggesting a strong impact of competition (Fig. 19). In particular, the initial weed biomass was high in all treatments and plots, where the initial crop biomass and competitive ability was low. This was the case in the cocksfoot crops, which generally showed a slower initial establishment than alfalfa and winter wheat (Fig. 18). Moreover, the autumn-sown perennial crops showed a better establishment than the spring-sown perennial crops. When these two ‘unfavourable factors’ were combined (spring-sown cocksfoot crops), initial weed biomass was highest (Fig. 18) and in turn reduced crop growth due to competition during the first month. However, the initial competitive disadvantages of spring sowing and of *Dactylis* crops disappeared already during the first year (Fig. 18).

- Weed biomasses decreased in summer (June-July 2007) both in the cut and the uncut treatments (Fig. 18), which was probably due to the high *Dactylis* and *Medicago* crop biomass.

- The reappearance of some weeds in *Medicago* crops in 2008 might be due to the reduced competition of this crop immediately after the cutting operations in contrast to *Dactylis*, where regrowth started immediately after cutting.

- The high impact of competition was also visible through the fact that big weed plants developed mainly in gaps of the crop canopy or when the perennial crop was experimentally removed on small sub-plots (data not shown).

- While the crop growth dynamics were similar for winter wheat and the autumn sown alfalfa in 2006/2007, all perennial crops had strong competitive advantages since 2007/2008 compared to the annual spring barley. Although spring barley was sown quite early in the year (February 2008), the development of a competitive vegetation cover was much quicker in the established perennial crops (Fig. 18). This was probably an important factor leading to very low absolute and relative weed biomasses in the perennial crops since the second year. In contrast, some weed species including *G. aparine*, *A. myosuroides*, *Polygonum spp*, *C. album* and *Sinapis arvensis* developed very high biomasses (per plant and per m^2) in the annual crop (Fig. 18), even causing crop yield reductions (data not shown).

Competition was thus probably an important factor for the decreasing weed biomasses in the perennial crops. This 'success' was the reason for the initial negative relation between crop and weed biomasses became weaker with time and disappeared in 2008 (Fig. 19).

C.II.4.3.3 Hay cuttings (C)

Hay cuttings present generally the only mechanical disturbances in PFCs. It destroys all plant organs above about 5 cm from the soil surface and may therefore considerably reduce biomass and seed production of tall weeds (Table 13). The impacts of cuttings on arable weeds are not frequently studied, probably as this kind of crop management is not very important in annual crops, which are mostly harvested only once per year with cutting heights that are often much higher than mowing of PFCs. In annual crops, cutting for crop harvest has thus probably limited impacts on weeds in contrast to the soil tillage operations applied after harvest. Therefore, the impacts of cuttings on weeds are mostly studied in the context of permanent

grasslands (Magda *et al.*, 2004; Hald, 2007), sometimes for set-aside fields (Dalbies-Dulout and Dore, 2001), but only rarely for temporary grasslands (Norris and Ayres, 1991; Hoveland *et al.*, 1996; Graglia *et al.*, 2006) or as (in-row) mowing treatments in annual crops used for weed control (Donald, 2007).

In our experiment, several indications show that hay cutting had strong impacts on weed population dynamics:

- The first 1-2 cutting operations in perennial crops after crop (and weed) sowing had strong negative effects on weed biomass (Fig. 18) suggesting that cutting enhanced the competitive advantage of perennial crops, who showed a quicker regrowth than most weeds.

- In reducing weed biomass and seed production, the cutting operations were probably an important factor causing the low weed plant densities in perennial crops compared to annual crops, who were cut only once per year (Fig. 12, Fig. 13).

- In contrast, modifying the cutting frequency in the perennial crops (3 *vs.* 5 cuts per year) caused relatively small effects (see above). When pooling all weed species, differences between the high and the low cutting frequency had no effects on the final weed densities. When looking at all measurement dates during the 2.5-years experiment, differences between the low and the high cutting frequency were only visible in alfalfa, where the lower frequency led to lower weed plant mortality rates and thus higher weed plant densities at the end of 2007 and increased weed biomass at the beginning of 2008. However, these weeds disappeared at the first hay cutting in May (Fig. 18). In cocksfoot, variations of the cutting frequency had no impacts, as weed densities were always very low (probably due to the dense superficial roots or other mechanisms suppressing weed emergence).

- Besides the differences between annual and perennial crops, cutting might have also caused some of the differences in weed plant and seed bank composition between spring and autumn sown crops. While autumn-sown crops were cut already twice in spring 2007 (27/4 and 7/6), the spring-sown crops were cut for the first time in summer (13/7) and some spring emerging species might have successfully produced seeds before.

C.II.4.3.4 Interactions between the three factors

Our results show that different mechanisms are probably at the origin of the high impacts of PFCs on weed populations (see summary in Table 13). These mechanisms acted often simultaneously and showed cumulative effects on the weed life cycle and several interactions. First, the absence of soil tillage (and of herbicides) favoured the development of very competitive crop canopies and root systems in the perennial crops suppressing weed growth, which corresponds to a positive interaction between the factors. Second, hay cuttings might temporarily alleviate the competition for light, which would correspond to a negative interaction. But our results do not support this hypothesis; the weeds did not profit from the temporally reduced competition for light. The competitive advantage of the forage crops appeared in particular *after* the first cutting treatments (corresponding to a positive interaction). The interaction between cuttings and competition depend thus strongly on the regrowth and re-establishment abilities of the different species. In our case, both *Dactylis* and *Medicago* crops had much better regrowth abilities than most of the weed species. The regrowth abilities of different weed and crop species as well as the interactions between cuttings and competition will be further analysed by specific experiments in controlled conditions in the following chapter C.III. Two results suggest that competition and cuttings are *both* required to obtain a good weed control in PFCs. First, weed biomasses were rather high *before* the first cutting treatment and decreased afterwards (Fig. 18). Second, some weed species developed very high biomasses on small sub plots, where the perennial crop plants were experimentally removed (data not shown).

C.II.4.4 Strength, limits, perspectives and preliminary recommendations

One strength of this experimental approach was to allow comparing different perennial crop management practices at the same time, which was rarely done in previous studies. Two crossing of important crop management factors (sowing season*crop species and cutting frequency*crop species) and the comparison to the succession of annual crops with different intercrop management practices permitted investigating some of the most important mechanisms underlying the impacts of PFCs on weeds.

Results indicated that the perennial crop sowing date has the strongest impact on weed communities among the three tested factors. However, such conclusions must be seed with caution, as variations in the experimental treatments (other sowing dates, crop species and cutting frequencies) might give different results. Futures studies might also integrate other perennial crop management factors such as fertilisation rate (Fan and Harris, 1996), cutting

height (Bell and Ritchie, 1989), cutting *dates* (adapted to crop or weed growth dynamics) and crop species mixtures (see below).

The high temporal resolution of the measurements permitted to follow the weed population dynamics on a much finer scale compared to the Chizé surveys and other previous studies, which often conduct only one or two evaluations of the weed density per year. Comparisons of this experimental study to the large-scale weed surveys on commercial fields showed that the weed community composition reacted in similar ways (see chapter D.I.1 of the general discussion for details). This increased the general value of this experimental study.

Four repetitions of each crop treatment on a rather small experimental site with rather homogeneous chemical soil conditions (except a gradients in the organic carbon and total nitrogen contents, Fig. 11) gave a sound basis for the comparisons. The enrichment of each plot with a defined quantity of weed seeds belonging to 17 annual weed species increased the homogeneity of the repetitions and reduced the number of quadrats where no weeds could be observed, increasing the statistical power. In future studies, it would be interesting to add also propagules of perennial weed species to the soil, species that had rather low natural densities in this experimental site. The plot size was rather small compared to some other studies, thus requiring specific soil tillage and forage cutting equipment adapted to the experimental plots, and the restriction to weed species that are not wind-dispersed. Two other facts moved this experiment away from the current agronomic reality:

- Only monospecific *Medicago*- or *Dactylis*- PFCs were included in this study, while both organic and conventional farmers often use **mixtures** of two or more grass and legume species. In our experiment *Medicago* and *Dactylis* crops had different temporal growth dynamics (including the speed of crop establishment, seasons of highest biomass production, regrowth speed after cuttings and plant longevity). The *Dactylis* stands showed a rather slow establishment, were very competitive in the middle of the experiment, presented very quick regrowth after the cuttings, but also first signs of senescence at the end. In contrast, *Medicago* stands were strong during the whole 2.5-years period, but had a slower post-cutting regrowth (compared to the *Dactylis* grasses). Other experiments indicated that resource use efficiencies and competitive abilities of crop species mixtures may be higher compared to monospecific crop stands due to ‘sampling effects’, ‘complementarity effects’ and ‘facilitation’, which may decrease the invasibility for weeds

including exotic species (Palmer and Maurer, 1997; Jiang *et al.*, 2007; Lanta and Leps, 2008).

- In our experiment, the cutting dates and frequencies followed the experimental plan of 3 *vs.* 5 cuts per year with *common* cutting dates for all treatments (Table 6). This design was used to disentangle the cutting frequency from the other experimental treatments (crop species, sowing date) and to avoid introducing other variables such as the exact cutting *dates* that may also be important for both crop and weeds growth. Cutting dates were thus not optimized to specific crop growth dynamics and phenological stages that differed between the crop species (*Medicago* and *Dactylis*), sowing dates and cutting frequencies (Fig. 18). It may thus be recommend to use a flexible cutting frequency and to adapt the cutting dates depending i) on the phenological stage of the forage crops to optimize the crop growth and to maximize crop-weed competition but also ii) on the phenological stage of the most noxious weed species to destroy high weed biomasses and to avoid seed production. In the case of our experiment, the lower cutting frequency showed some advantages:

    - the *Dactylis* crops produced significantly more biomass than under the high frequency (equal production for *Medicago*, Fig. 17),
    - very frequent cuttings may reduce the regrowth ability of *Medicago* crops,

  However, the cutting frequency should also not be too low, which may increase the risk of high weed seed production and may lead to inferior forage quality.

While the weed seed bank analyses gives a good indication of the long-term effects of PFCs on weed infestations, this should also be verified by long-term crop rotation experiments such as the studies of Andersson & Milberg (1998) and Sosnoskie *et al.* (2006). Moreover, the findings may depend on climate and soil conditions and must thus be repeated in other locations. While such huge studies were not possible in our case, the effects of the perennial and annual crops on the weed infestation of the following crop will be tested on our experimental set up by a) analyzing the soil seed bank and by observing the weed vegetation in a following test crop sown on all experimental plots.

C.III REGROWTH AFTER CUTTING

C.III.1 **Article 4:**

Meiss, H., Munier-Jolain, N., Henriot, F. & Caneill, J. (2008b) Effects of biomass, age and functional traits on regrowth of arable weeds after cutting.

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Effects of biomass, age and functional traits on regrowth of arable weeds after cutting

Einfluss von Biomasse, Alter und funktionalen Eigenschaften auf das Wachstum von Ackerunkräutern nach Schnittmassnahmen

H. Meiss*, N. Munier-Jolain, F. Henriot & J. Caneill
INRA, UMR1210 Biologie et Gestion des Adventices, 17 rue Sully, BP 86510, F-21065 Dijon cedex, France
* Corresponding author, helmut.meiss@dijon.inra.fr

Summary

In sown field margin stripes or pluriannual forage crops, arable weeds are exposed to high competition and regular mowing or hay cutting, to which they may react very differently. A greenhouse experiment permitted to understand some key factors shaping the ability of common arable weeds and forage crops to grow after such cuttings. Even without competition, cutting shoots at 5cm height reduced biomass production of all 10 species studied, but 6 annual broadleaf weeds were much more affected than 2 perennial forage crops (*Dactylis, Medicago*) and 2 annual grasses (*Alopecurus, Bromus*), confirming our hypothesis. Variation of regrowth speed within each species was always positively related to the plant size before cutting, suggesting that bigger plants can remobilize more belowground resources. But this is only true for plants sown at the same date, as older weeds showed reduced regrowth despite their bigger size. Carbohydrate resources of older plants might have already been depleted for reproductive growth. This basic knowledge may be used to construct weed demography models and to develop innovative cropping systems. If most annual weeds cannot grow and reproduce when cut under real conditions with competition, introducing mown temporary grasslands into crop rotations may readily be used as an element of Integrated Weed Management.

Key words: compensatory growth, defoliation, forage crops, integrated weed management, mowing, resprouting, regrowth dynamics, remobilization, temporary grassland.

Zusammenfassung

In Ackerrandstreifen und mehrjährigen Futterkulturen sind Ackerunkräuter häufig einem hohem Konkurrenzdruck und regelmäßigen Schnitten ausgesetzt, worauf sie sehr verschieden reagieren können. Ein Gewächshausexperiment ermöglichte es, einige der Faktoren besser zu verstehen, die den Wiederaustrieb von Ackerunkräutern nach solchen Schnitten beeinflussen. Experimentelles Entfernen der Triebe in 5 cm Höhe reduzierte die Biomasseproduktion aller 10 untersuchten Arten. Allerdings litten 6 breitblättrige Unkrautarten mehr unter den Schnitten als 2 ausdauernde Futterkulturen (Knaulgras, Luzerne) und als 2 einjährige Gräser (Ackerfuchsschwanz, Taube Trespe), was unseren Erwartungen entsprach. Die Wachstumsgeschwindigkeit nach dem Schnitt konnte bei fast allen Arten sehr gut durch die Biomasse vor dem Schnitt erklärt werden. Dies deutet darauf hin, dass größere Pflanzen mehr unterirdische Ressourcen für den Wiederaustrieb mobilisieren können als kleinere. Dies ist jedoch nur der Fall für Pflanzen, die gleichzeitig gesät wurden, da ältere Pflanzen weniger gut nachwuchsen als erwartet. Die für den Wiederaustrieb notwendigen Ressourcen könnten bei älteren Pflanzen teilweise schon zur Blüten- und Samenproduktion verbraucht worden sein. Diese grundlegenden Erkenntnisse können einerseits hilfreich sein zur Entwicklung von Unkrautpopulationsmodellen, andererseits zur praktischen Gestaltung von innovativen Ackerbausystemen. Wenn einjährige Unkräuter durch regelmäßige Schnitte und hohe Konkurrenz in mehrjährigen Futterkulturen stark unterdrückt werden, könnte der Herbizideinsatz in angepassten Fruchtfolgen stark reduziert werden.

Stichwörter: Kompensation, integrierter Pflanzenschutz, Luzerne, Mahd, mechanische Unkrautkontrolle, Mobilisierung von Ressourcen, Temporäres Grünland, Wachstumsdynamik.

1 Introduction

Plants may respond very differently to physical damage and loss of aboveground organs caused by natural disturbances like herbivory, frost, drought, wind break or anthropogenic disturbances like mowing (Iwasa and Kubo 1997). Responses may range from death of the plant to full recovery (or even overcompensation) *via* compensatory regrowth (Belsky 1987). When leaf area has strongly been reduced, the plant runs out of assimilation products (carbohydrates like sugar) (Smith et al. 1989; Hume 1991). To ensure survival and reproduction after defoliation, new leaf area must quickly be installed to restore a 'functional equilibrium' between shoot and root biomass (Poorter and Nagel 2000). This can be achieved by aboveground regrowth, but the plants have to cope with two problems: photosynthesis is reduced or absent and apical meristems may be destroyed (Iwasa and Kubo 1997).

As individual plants and species may react differently according to their specific traits, grazing and mowing may have strong impacts on population demography and community composition (Diaz et al. 2007). The regrowth capacity is not only important for plants in pastures and perennial grasslands, but also for weeds in arable systems. Arable weeds may be subjected to mowing in field margin stripes (De Cauwer et al. 2005), temporary grasslands (pluriannual forage crops rotated with annual crops), or set asides (Dalbies-Dulout and Dore 2001) as well as during harvest of most annual crops. Moreover, in-row mowing may successfully be used as part of Integrated Weed Management in arable crops (Donald 2000). In all these situations, mowing may be used to manage the spontaneous vegetation. Environmental problems associated with conventional weed control using either herbicides or soil tillage do not exist with mowing: there is neither groundwater contamination nor increased nutrient leaching and soil erosion risk (Donald 2000). If soil tillage may stimulate the emergence of new weeds, this is not the case for mowing. To predict weed responses to cuttings, and to effectively use this technique in farming practice, we need more knowledge about the factors shaping regrowth ability. But data on regrowth of weeds are scarce in contrast to data

Tab. 1: Overview of hypothetical factors and underlying variables affecting regrowth of weed plants after cutting and methods used in this study to manipulate the variables.

Tab. 1: Übersicht der hypothetischen Faktoren und zugrunde liegenden Variablen des Wachstums von Unkrautpflanzen nach einem Schnitt und der in dieser Studie angewandten Methoden zur Manipulation dieser Variablen.

Factor affecting regrowth ability							
A) Total or relative green area remaining for photosynthesis							
	B) Quantity of C and N resources that can be remobilized						
		C) Presence of intact apical buds after cutting					
			D) General growth factors & growth conditions				
				Variable underlying the factors	**Examplary References**	**Role in this study**	**Methods and modalities used in this study**
A	**B**	**C**		**Species** (& genotype)	4, 8, 9, 10	**tested**	**8 weed & 2 forage crop species**
A		C		cutting height	1, 2, 4, 7, 10	standardized	always cut at 5 cm from soil surface
A	B			cutting date	1, 2, 3, 7	standardized	see Fig. 1
	B	C		cutting frequency	1, 3, 5, 6, 7, 11	standardized	see Fig. 1
A	**B**			**plant size (biomass)**	8, 10	**tested**	**large range (created by shadowing)**
A		C		**plant morphology**	10	**(tested)**	**test of natural variance**
A	**B**			**plant age** & stage	1, 2, 4, 7	**tested**	**3 ages (created by diff. sowing dates)**
	B		D	soil & climate variables, parasitism, competition, symbioses, crop & weed management,…	4, 5	standardized	good growth conditions without competition in controlled experiment

Variables tested in this study are highlighted in **bold**.

[1] (Hume 1991), [2] (El-Shatnawi et al. 1999), [3] (Donald 2000), [4] (Andreasen et al. 2002), [5] (Dalbies-Dulout and Dore 2001), [6] (Kluth et al. 2003), [7] (Magda et al. 2004), [8] (Vesk et al. 2004), [9] (De Cauwer et al. 2005), [10] (Mager et al. 2006), [11] (Lestienne et al. 2006).

of forage crop species that are repeatedly cut or grazed, such as clover, lucerne (Smith et al. 1989), and grasses (Davidson and Milthorpe 1966; Lestienne et al. 2006).

Many variables have been proposed to have an influence on the ability of plants to grow and reproduce after physical destruction of aboveground biomass. For simplicity, we propose to assign these variables to four groups of **functional factors** based on regrowth mechanism. A summary of the factors and the underlying variables with some exemplary references are given in Table 1. Obviously, there may be many interactions between the different variables.

A) The most important factor shaping regrowth is likely to be the (absolute or relative) **quantity of leaf area** (photosynthetically active tissues) remaining after destruction (Tab. 1). This quantity is first of all determined by the *intensity of defoliation*, *i.e.* the *height* and *frequency* of *mowing*, (El-Shatnawi et al. 1999; Andreasen et al. 2002; Lestienne et al. 2006). But it also depends on the *size* and *morphology of the plants*, which may differ *between* and *within species* (Mager et al. 2006).

B) Plants need C and N resources for regrowth. As photosynthesis is strongly reduced, regrowth may only be possible if enough **nonstructural carbohydrate resources** can be remobilized from roots and stubbles (Tab. 1). This mechanism has been studied for different forage crops: *Dactylis* (Davidson and Milthorpe 1966), *Medicago* (Smith et al. 1989) and *Lolium* (Lestienne et al. 2006), but not on weeds. The amount of carbohydrate resources available for remobilization is likely to depend on *species functional type* (*i.e.* geophytes with belowground storage organs vs. therophythes with simple roots). Within one species, the amount of stocked reserves might be related to *(belowground) biomass* [positive relation], and to the *age* or *phenological stage* of the plant [Hump-shaped relation: very young plants might not yet have accumulated many resources and very old plants might have already remobilized most of them for flowering and seed production, Magda et al. (2004)]. The resources may also be depleted if plants have already been damaged previously due to a higher *cutting frequency.* (It has been shown that repeated cutting reduces carbohydrate resources of *Cirsium arvense* (Kluth et al. 2003; Graglia et al. 2006), *Bromus willdenowii* and different *Lolium* species (Hume 1991)).

C) Regrowth may be more difficult if most of the **apical meristems** are destroyed, a phenomenon called 'meristem limitation' (Mager et al. 2006). The *vertical position of apical meristems* and of *inactive axillary buds* should be the underlying variables in interaction with the *cutting height* (Tab. 1). The functional group of grasses may be advantaged over broadleaf species, as their meristems are located closer to the soil surface. This difference may be one reason for the observed replacement of broadleaf weeds by grasses on mown field margin stripes (De Cauwer et al. 2005).

D) Within the last group of factors shaping regrowth performance, we assort all types of external **growth factors** (*light/PAR*, *nutrient* and *water* availability) as well as all **growth conditions** (*temperature*, *photoperiod*, *pathogene attack, competition, crop and weed management,…*) which determine the general performance of plants. Regrowth would be slower or impossible if a growth factor is reduced, *i.e.* due to *competition* (Kluth et al. 2003), or if growth conditions are not optimal for the species.

Given this complexity of interacting factors, weed species can probably not simply be classified according to a dichotomy opposing 'sprouders' (species able to regrow) and 'non-sprouders' (Vesk et al. 2004). A continuous variation of the regrowth ability is more likely. Nevertheless, basic differences may be found between species with different functional traits. Mowing may have less severe impacts on species with some key characteristics such as a perennial life cycle, the possibility for vegetative reproduction, belowground storage organs and a flat morphology with meristems (buds) near or underneath the soil surface. Species with opposite characteristics may be more penalized by mowing, although

relations are not necessarily simple (Vesk et al. 2004). For example, very short-living plants might also be *favored* if they can complete their life cycle between two consecutive mowing interventions.

The principal aim of this study was to acquire knowledge on the regrowth ability of different weed and crop species and the influence of some variables while standardizing many others (Tab. 1). We recorded growth dynamics of individual weed plants after four consecutive cutting treatments. The emphasis lies on the understanding of some basic regrowth mechanisms. A second aim of this study (not reported here) is to obtain some knowledge and parameter values to construct a model of regrowth dynamics, which may be integrated into a weed demography model Alomy-Sys/FlorSys (Colbach et al. 2007).

From the list of hypothetical variables (Tab. 1), we investigated the influence of (1) *species*, (2) *plant size* and (3) *plant age* on the regrowth ability of weeds. Several hypotheses will be tested: (H1a) Regrowth is stronger for perennial (forage) species compared to annual weeds. (H1b) Grasses perform better than broadleaf weeds. (H2) Bigger plants show faster initial regrowth than smaller plants (of same age), as they may have more carbohydrates stocked in roots and stubbles. (H3) Older plants show slower regrowth speed, as aboveground resources are already remobilized for generative growth. (Alternatively, very young plants may be disadvantaged, as they have not yet accumulated much belowground resources).

2 Materials and methods

Experimental Design and Growth Conditions. A greenhouse experiment was carried out in Dijon (Eastern France, 5°02'E, 47°20'N). To test the 1st hypothesis, 8 common weeds species and 2 forage crop species frequently cultivated in temporary grasslands were selected, each group contained both grass and broadleaf species (see Tab. 2 for species names). Seeds were obtained from Herbiseed, Twyford, Berkshire, UK (http://www.herbiseed.com). Seeds were planted on 02–02–2007 in large plastic pots filled with 5 liters of substrate (3/4 fertile potting soil + 1/4 sand) and thinned out later to keep only one plant per pot. Those conditions were expected to minimize competition. Pots were regularly watered. Due to the big quantity of fertile substrate, no supplementary fertilization was applied during the experiment. Pots were placed in a glasshouse until May, which was only heated to prevent frost; afterwards, pots were placed open air.

To test the 2nd hypothesis (effect of biomass), we (successfully) increased the variance of plant size by placing 4 plants of all 10 species under partial shadow until the 1st cutting, while 4 other plants grew in normal sunlight (Fig. 1). We assumed that above- and belowground biomasses are correlated (Poorter and Nagel 2000).

The 3rd hypothesis (effect of plant age) was tested only on two weed species (*A. myosuroides* and *S. media*). Seeds were sown at 3 different dates separated by about 3 weeks from each other (12–01, 02–02, 23–02–2007) to obtain 3 contrasted ages at the time of the 1st cutting (02–04, illustrated in Fig. 1).

Cutting Treatment. All plants were cut at a unique date (02–04–2007) and at a standardized height (about 5 cm above the soil surface) using a pair of scissors. Shoots of reptant plants were carefully lifted up before cutting. As a control, 4 supplementary plants of each species were leaved uncut to compare their productivity with the cumulated productivity of cut plants (Fig. 1). The cutting treatment was repeated at four dates separated by 4–6 weeks, *i.e.* regrown shoots were repeatedly removed at the same height (see Fig. 1 for the cutting dates). For each species and experimental modality, we used 4 replicate plants.

Data Collection. Non-destructive measures were used to record regrowth dynamics *between* the cuttings and destructive measures *at* each cutting date. (For the "destructive" measures, we could use the plant material removed by experimental cutting. Therefore, the same plants could be kept for all consecutive mowing treatments.)

Image analysis of digital pictures permitted to calculate the *horizontally projected plant surface*. Pictures were taken weekly from each plant under standardized light conditions from about 1 m above the plant ('top view') using a digital reflex camera (Canon EOS 350D, 8 mega pixel). Based on colour and brightness thresholds, the image analysis software Visilog 5.4 (Noesis, Les Ulis, France) discriminated pixels belonging to the plant and pixels belonging to the contrasted background (a red drapery placed around the stems underneath the plant's canopy). Plant surfaces were calculated by comparing the numbers of pixels belonging to the plant with the number of pixels belonging to a white card of known surface.

Tab. 2: Names of the weed and crop species used and values of the 'regrowth ratio'.

Tab. 2: Namen der verwendeten Unkraut- und Kulturarten und Proportion der Wachstumsleistung von geschnittenen im Verhältnis zu ungeschnittenen Pflanzen.

Weed & crop species				Group			Regrowth ratio[2]
CODE	Scientific name	English name	German name	Life cycle	Role	Nb of cotyl.[1]	
BROST	*Bromus sterilis* L.	barren brome	Taube Trespe	annual	weed	**1**	0.912 a
ALOMY	*Alopecurus myosuroides* Huds.	blackgrass	Acker-Fuchsschwanzgras	annual	weed	**1**	0.556 ab
Dactylis	*Dactylis glomerata* L.	cocksfoot grass	Gewöhnliches Knäuelgras	perennial	crop	**1**	0.543 ab
Medic.	*Medicago sativa* L.	lucerne (alfalfa)	Luzerne	perennial	crop	**2**	0.539 ab
CAPBP	*Capsella bursa-pastoris* Medi	shepherd's-purse	Hirtentäschelkraut	annual	weed	**2**	0.529 ab
AMBEL	*Ambrosia artemisiifloia* L.	ragweed	Beifußblättrige Ambrosie	annual	weed	**2**	0.508 ab
STEME	*Stellaria media* (L.) Vill.	common chickweed	Vogel-Sternmiere	annual	weed	**2**	0.481 ab
CHEAL	*Chenopodium album* L.	fat hen	Weißer Gänsefuß	annual	weed	**2**	0.414 b
VERPE	*Veronica persica* Poiret	ivy-leaved speedwell	Persischer Ehrenpreis	annual	weed	**2**	0.317 b
AMARE	*Amaranthus retroflexus* L.	common amaranth	Zurückgebogene Amarant	annual	weed	**2**	0.103 b

[1] Number of cotyledons opposing (**1**) grasses and (**2**) broadleaf species.

[2] The '*regrowth ratio*' was calculated as follows: (biomass grown before 1st cut + biomass regrown after 1st cut) / mean biomass of uncut plants. Data for plants grown in light. Mean values followed by same characters are not significantly different at α=0.05.

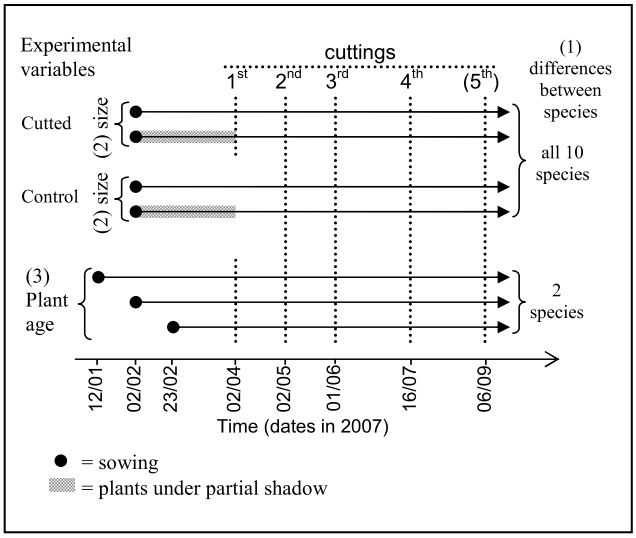

Fig. 1: Overview of the experimental variables and treatments, sowing and cutting dates.

Abb. 1: Übersicht der experimentellen Variablen, Aussaat- und Schnittterminen.

Each vertical line represents an experimental modality with four plants of each species (n = 4). The 5th cutting is only used to evaluate regrowth of after the 4th cutting.

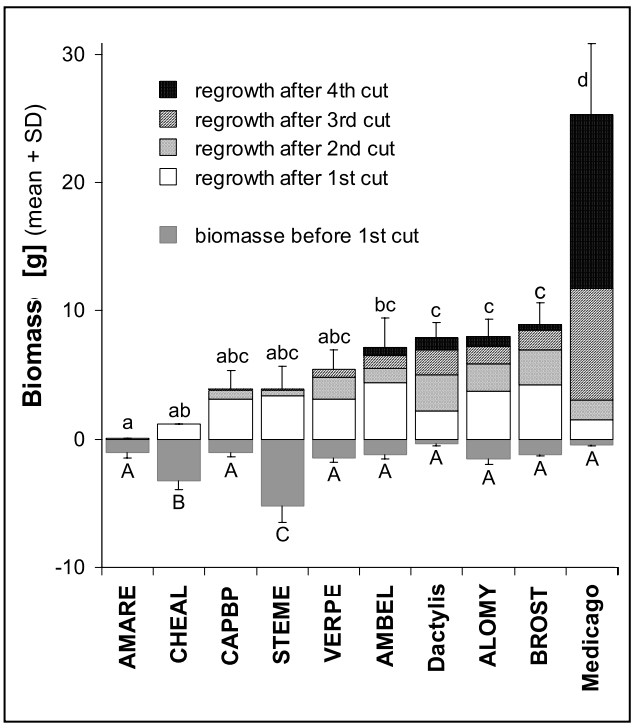

Fig. 2: Regrowth capacity of different weed and crop species after 4 successive cuttings.

Abb. 2: Wachstum verschiedener Unkraut- und Kulturarten nach 4 aufeinander folgenden Schnitten.

Charts represent mean weights of cutted aboveground dry matter (g/plant, n = 4). Error bars represent 1SD of the 'total regrowth' after 4 cuttings (= sum of the positive charts). Absence of charts indicates that plants did not survive after the last cut. Negative charts represent biomass (mean & 1SD) before the 1st cutting. Charts connected by same characters are not significantly different at α = 0.05.

The absolute regrowth performance after each cut was recorded at the next cutting date by recording *leaf area* and *biomass*. Leaf area was measured by depositing the cut material (leaves and stems) in an area meter (LI-3100, LI-COR inc. Lincoln, Nebraska, USA). Biomass was weighed after drying the cut material at 80°C for 48 h. The projected plant surface obtained by image analysis was highly correlated to the 'real' leaf area (R^2 ranging from 0.78 to 0.98 depending on species, mean R^2 = 0.92), validating the non-destructive measurement. As the two destructive measurements (biomass and "real" leaf area) were highly correlated too, we will only present the results for biomass.

Data Analysis. To compare biomass production of cut and uncut plants, a *'regrowth ratio'* was calculated as follows: (biomass before the 1st cut + biomass regrown after the 1st cut) / biomass of uncut plants at the same time. An *'initial regrowth speed'* was calculated as the difference between the projected plant surface 8 days after cutting and the projected plant surface immediately after cutting ('residual surface'). We used one-way ANOVA on untransformed data with species or experimental treatments as fixed effects. If the effect was significant at α = 0.05, post-hoc tests for multiple comparisons of means (Tukey's HSD) were used. Simple and multiple linear regression models were fitted to explain 'regrowth speed' by the plant size (projected surface) before cut and by the 'residual surface' immediately after cut. Statistical analyses were done using Systat 11 (Systat Software Inc.) and JMP 5.0.1.2 (SAS Institute Inc.).

3 Results

3.1 Species differences (H1)

All 10 species suffered from the cutting treatment, regardless of their growth conditions before cut (full light or partial shadow): uncut plants produced always more biomass than cut plants, even when biomass grown before cut and regrown biomass were added together. The '*regrowth ratio*' was thus always below 1 (Tab. 2), no species showed full recovery or overcompensation. But the '*regrowth ratio*' showed significant differences between the 10 species ($F_{9,30}$ = 11.87, p < 0.0001), ranging from 0.91 for *B. sterilis* (overall biomass production of cut plants approaching that of uncut plants) to only 0.10 for *A. retroflexus* (Tab. 2). Hardly any regrowth was detected for this species (Fig. 2).

Important differences between the 10 species were also detected for the '*initial regrowth speed*' after the first cut ($F_{9,30}$ = 4.63, p = 0.0007, see Tab. 3 for species mean values). There was a slight positive correlation between '*regrowth ratio*' and '*initial regrowth speed*' for the species mean values (R^2 = 0.55, t = 1.85, $P_{1\text{-tailed}}$ = 0.051) and species ranking was nearly conserved (compare Tab. 2 and 3). Species thus tended to react in a similar way to those two parameters.

Species differences were strongest if the cumulated biomass production after the 4 successive cuttings, '*total regrowth*' was considered ($F_{9,30}$ = 29.41, p < 0.0001; see Fig. 2 for illustration and discrimination of species means). '*Total regrowth*' was strongly influenced by the biomass production after the 3rd and 4th cuttings, which were highest for the perennial *M. sativa*, much lower for the three grasses, but nil for most of the annual broadleaf weeds (Fig. 3). Some of the broadleaf weeds even died before the end of the experiment: *A. retroflexus* plants already died after the 1st cutting, *C. album* between the 2nd and 3rd, *C. bursa-pastoris* and *S. media* between the 3rd and 4th cutting and *V. persica* after the 4th cutting (Fig. 2). The mean quantity of '*total regrowth*' was not correlated with '*initial regrowth speed*' after the first cutting (R^2 = -0.038, t = -0.11, $P_{1\text{-tailed}}$ = 0.54) and only slightly correlated with '*regrowth ratio*' (R^2 = 0.39, t = 1.22, $P_{1\text{-tailed}}$ = 0.128).

Tab. 3: Simple and multiple regressions explaining initial regrowth speed for 10 species.
Tab. 3: Einfache und multiple Regressionen der Wachstumsgeschwindigkeit bei 10 Arten nach einem Schnitt.

Species CODE[1]	Regrowth speed[2]	Simple regression[3]			Multiple regression[4]			Selected model[5]
		R^2	$F_{(1,7)}$	p	R^2	$F_{(2,6)}$	p	
ALOMY	94.77 a	0.96	150.39	0.000	0.97	118.77	0.000	simple
BROST	59.78 ab	0.97	232.97	0.000	0.97	109.65	0.000	simple
STEME	54.68 abc	0.58	9.78	0.017	0.97	126.50	0.000	multiple
CAPBP	50.12 bcd	0.84	36.89	0.001	0.89	29.14	0.001	simple
Dactylis	25.00 bcde	0.96	180.42	0.000	0.99	240.13	0.000	multiple
VERPE	23.18 bcde	0.46	6.04	0.044	0.73	9.77	0.013	multiple
AMBEL	11.90 cde	0.49	6.68	0.036	0.51	4.19	0.073	simple
Medicago	7.88 de	0.69	15.37	0.006	0.70	8.76	0.017	simple
CHEAL	4.55 e	0.13	1.06	0.338	0.81	15.10	0.005	multiple
AMARE	0.02 e	0.01	0.04	0.839	0.00	0.08	0.928	none

[1] See Tab. 2 for species names.
[2] Mean '*initial regrowth speed*' of plants grown in light (= net absolute increase of the projected plant surface in mm² during 8 days after the 1st cutting). Mean values followed by same characters are not significantly different at α = 0.05.
[3] Simple linear regression models, where '*initial regrowth speed*' is explained by plant size (projected plant surface in mm²) *before* cutting. Given are the adjusted regression coefficients (R^2), the *F*-ratios and the associated probabilities *p*. Regressions not significant at p = 0.05 are shaded in grey. The regression for ALOMY is illustrated in Fig. 3.
[4] Multiple linear regression models, where the '*residual plant surface*' (projected surface remaining *immediately after* cutting) is entered as a second explanatory variable.
[5] The model with the higher *F*-ratios is selected, if it is significant. By introducing residual plant surface, models were (slightly) improved for 4 out of 10 species. None of the models fit to AMARE, as regrowth speed was nearly zero.

3.2 Plant size before cutting (H2)

As desired, the shading treatment on half of the plants successfully increased the variability of plant sizes (surfaces and biomasses before 1st cutting) of all 10 species. Plant size before cutting had a positive influence on regrowth speed of all species. As hypothesized, bigger individuals showed faster regrowth than smaller ones. Simple linear regression models explain 46–97% of the variance of regrowth speed by the plant surface *before* cutting (Tab. 2). By introducing the '*residual plant surface*' remaining immediately after cutting as a second explanatory variable into the regression models, predictions (slightly) could be improved for 4 out of 10 species (Tab. 2). Besides '*initial regrowth speed*', such simple linear regressions could also explain the *biomass* regrown after the 1st cutting (R^2 ranged from 0.36 to 0.91 depending on species). In contrast, the sum of biomasses regrown after all 4 cuttings ('*total regrowth*') could not be explained by plant size before the 1st cut (which had not been expected in any case).

3.3 Plant age (H3)

The plants sown at different dates had different sizes at the time of the 1st cut but were all still in vegetative stages. *A. myosuroides* plants sown three weeks earlier than the rest of the experiment (Fig. 1) showed lower regrowth speed than expected by the strong regression between regrowth speed and plant size before cut (illustrated in Fig. 3). In a similar way, plants sown three weeks later showed higher regrowth speed than expected, but differences were smaller (Fig. 3). The regrowth speed of *S. media* did not show such a clear effect of plant age. Nevertheless, plant age had a strong influence on '*total regrowth*' for both species: Older plants yielded significantly less biomass than younger plants (Fig. 4). The response of biomass regrowth to the plant age was higher after the 2nd, 3rd and 4th cuttings than after the 1st cutting. Younger plants survived more cutting treatments than older plants. None of the plants sown at the first date survived all four cuttings (Fig. 4).

4 Discussion

The experimental cutting treatments had negative impacts on all species in all situations, as we never observed full recovery. This is in agreement with many authors, although exceptions may exist (Belsky 1986). In a similar study, Andreasen et al. (2002) observed partial recovery rates for *Avena fatua*, *Galeopsis tetrahit* and *Polygonum convolvulus*, overcompensation (128%) occurred only for *Galium aparine*, if cutting height was at maximum (8 cm) and plant age at minimum. Mager et al. (2006) observed different partial recovery rates for *Amaranthus rudis* and *Ambrosia trifida*, whereas *Iopeda hederacea* sometimes showed full recovery.

The negative impacts of cutting observed in our experiments are expected to be even stronger if plants would be submitted to inter- or intraspecific competition, *i.e.* in a dense forage crop, or to stress. It has been shown that regrowth after cutting is slowed down if *Cirsium arvense* has been infected by a pathogen (Kluth et al. 2003).

4.1 Species differences (H1)

Though all species suffered from the cuttings and produced less biomass compared to uncut plants, there were considerable differences between the species. The results correspond to our two hypotheses: perennial forage species performed better than annual weeds and grasses better than broadleaf weeds (Fig. 2). *M. sativa* showed by far the highest '*total regrowth*', followed by the three grassy species. The six annual broadleaf weeds had the lowest shoot biomass production after the successive cuttings and sometimes even died (Fig. 2).

The ranking of the ten species was slightly modified when considering '*initial regrowth speed*' and '*regrowth ratio*'. For these two variables, the grasses showed higher values then *M. sativa,* who performed more like the other broadleaf species (Tabs. 2 & 3). This may be surprising, as cultivated lucerne has been bred for tolerating regular cuttings (Smith et al. 1989). We observed that regrowth of all broadleaf species (including lucerne) only started about 4–7 days after cutting, whereas the grassy species already showed considerable leaf elongation few hours later. These results confirm the hypothesized disadvantage of broadleaf species, where the apical meristems are destroyed or damaged by cutting and regrowth must start from axilary buds (Mager et al. 2006). In contrast, grasses may directly continue regrowth, as their apical meristems at the plant base are not touched by hay cutting. Our results suggest that the superiority of the two perennial species over annuals only appeared after the 2nd cutting (Fig. 2).

Observed differences in regrowth ability *within* the group of annual broadleaf weeds (Tab. 2 & 3, Fig. 2) may originate from two effects, which are both related to plant morphology: **(1)** The plant size and the vertical distribution of leaf area may cause differences in the amount of destroyed leaf area (Mager et al. 2006). Tall species with an upright morphology like *A. retroflexus* and *C. album* suffered more from the cuttings than reptant species like *V. persica* and *S. media* or species forming a rosette like *C. bursa-pastoris*, although we cutted the reptant shoots too. This effect is thus expected to be even stronger in real fields, where reptant shoots may stay completely undestroyed. **(2)** The quantity of (dormant) axillary buds remaining below cutting level may be a second reason. Indeed, the two reptant species *V. persica* and *S. media* had many secondary shoots and therefore potentially more axillary buds near the soil surface than the erected species. If the species with an upright morphology and only one or few main stems are cut too low, buds for compensatory growth may be lacking, which has been reported to be important for regrowth of semi-arid plants (Vesk et al. 2004). This might explain the "sudden death" observed here for some plants of *A. retroflexus* and *C. album,* whereas some other plants of the same species were able to resume growth some days after cutting. Surprisingly, *A. artemisiifolia* performed better than *A. retroflexus* and *C. album* (Fig. 2, Tab. 2) despite its similar morphology. Following (Vincent and Ahmim 1985), cutting of the invasive *A. artemisiifolia* is only effective if plants are either cut very close to the ground surface or when flowering has already started. Both were not the case here.

4.2 Plant size before cutting (H2)

We hypothesized that bigger plants may have more carbohydrate resources available for regrowth after cutting. This hypothesis is largely supported by our results showing highly significant linear regressions of regrowth speed on plant size before cutting. This was the case for all species studied, except for two species where many plants died directly after the 1st cutting (Tab. 3). Mager et al. (2006) observed somehow similar positive effects of plant size on regrowth speed of *Ipomoea hederacea,* but no significant effects for *Amaranthus rudis* and *Ambrosia trifida*.

Introducing the residual plant surface remaining after cutting as a second explanatory variable sometimes improved the regression models. This was for example the case for the reptant species *V. persica* and *S. media*, where this variable showed some variation caused by differences in plant morphology. In these cases, the variance explained by plant size before cutting was lowered. This is consistent with the deduction suggesting that remobilization of belowground

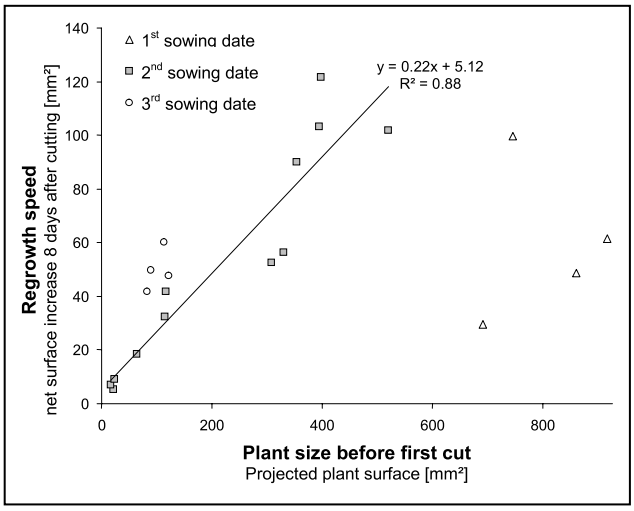

Fig. 3: The impact of plant age (sowing date) on the 'initial regrowth speed' of A. myosuroides.

Abb. 3: Der Einfluss des Pflanzenalters (Aussaatdatum) auf die Geschwindigkeit des Wiederaustriebs von Ackerfuchsschwanz.

Plant size before cut is a good predictor for 'regrowth speed' (linear regression for plants of the 2nd sowing date, grey □). Older plants (△, 1st sowing date) showed a much lower regrowth speed than expected after this regression, whereas younger plants (○, 3rd sowing date) showed a higher regrowth speed than expected.

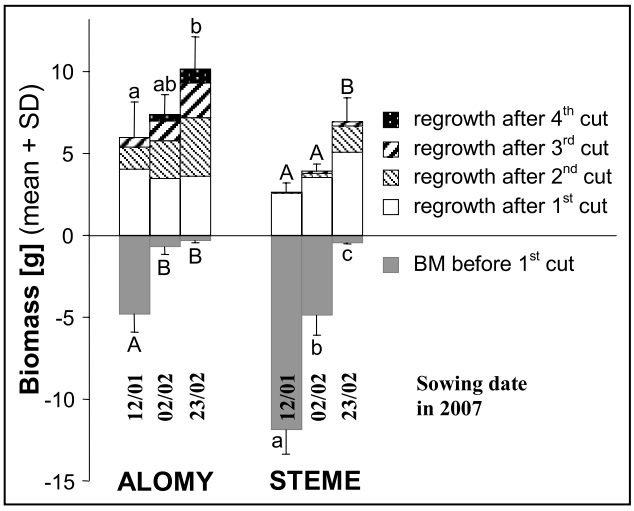

Fig. 4: Impact of age on regrowth capacity of two weed species after 4 successive cuttings.

Abb. 4: Einfluss des Alters auf die Geschwindigkeit des Wiederaustriebs von zwei Unkrautarten nach 4 aufeinanderfolgenden Schnitten.

Charts, hatchings and error bars as in Fig 2. Sowing dates of one species connected by the same characters are not significantly different at α = 0.05. Older plants produced less biomass after 4 cuttings. Younger plants showed higher regrowth rates, especially after the 2nd, 3rd and 4th cuttings. None of plants sown at the first date survived all 4 cuttings (absence of charts), *i.e.* older plants died earlier, especially if they already started flowering and seed production before the last cut (data not shown).

resources is more important if the leaf area has strongly been reduced by cutting.

4.3 Plant age (H3)

We observed a decreased regrowth speed and a lower total biomass production for older plants compared to plants sown 3 and 6 weeks later. This agrees with the assumption that older plants already used some of their stocked carbohydrate reserves for flowering and seed production, but not with the idea that very *young* plants would show reduced regrowth. Within the investigated range of the two species studied, a linear decrease of the regrowth ability with plant age is thus more likely than a hump-shaped relation. Andreasen et al. (2002) did not observe significant effect of plant stage on biomass production after cutting. They concluded that the stages compared in their experiment were too close together. In that way, the differences observed here are interesting, as plants were still in vegetative stages, at least at the 1st cutting date. Therefore, regrowth speed is expected to be even lower for older plants at reproductive stages. A broader range of plant ages would be necessary to confirm this issue more thoroughly.

4.4 Conclusion and applications

With this experimental approach, we were able to confirm some hypotheses about the factors shaping regrowth of weeds. By comparing the performance of 10 different species, we confirmed some functional differences between annual weeds and perennial forage crops as well as between grasses and broadleaf species. Additionally, we observed some differences *within* annual broadleaf weeds never reported before, that may also be based on plant morphological traits such as the vertical distribution of leaf area and the position of buds necessary for regrowth. By separating the (opposed) effects of plant size and plant age before cutting, we demonstrated that both factors might be related to the quantity of resources that can be remobilized.

These results provide useful information about the mechanisms and factors affecting regrowth. This is necessary for the construction of weed demography models. It may also be used for developing innovative cropping systems based on Integrated Weed Management. Weed regrowth after mowing is an important factor of weed suppression in temporary grasslands or sown field margin stripes. The basic knowledge gained from this experiment might be extended by analyzing the combined effects of cuttings and competition caused by regrowing grass swards or forage crops.

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C.III.2 **Article 5:**

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Cutting and competition reduce weed growth: additive or interactive effects?

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XIIIème COLLOQUE INTERNATIONAL SUR LA BIOLOGIE DES MAUVAISES HERBES

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CUTTING AND COMPETITION REDUCE WEED GROWTH: ADDITIVE OR INTERACTIVE EFFECTS?

H. MEISS[1,2], R. BONNOT[1], F. STRBIK[1], R. WALDHARDT[2],

J. CANEILL[1], N. MUNIER-JOLAIN[1]

[1] Institut National de la Recherche Agronomique (INRA), UMR 1210 Biologie et Gestion des Adventices, 17 rue Sully, BP 86510, F-21065 Dijon cedex, France.

[2] Institute of Landscape Ecology and Resources Management, Justus-Liebig-University Giessen, IFZ, Heinrich-Buff-Ring 26-32, D-35392 Giessen, Germany.

E-mails: helmut.meiss@dijon.inra.fr, remi_bnt@hotmail.com, rainer.waldhardt@umwelt.uni-giessen.de, jacques.caneill@dijon.inra.fr, munierj@dijon.inra.fr

SUMMARY:

Weed growth may be affected by disturbance or competition. Both processes are important in pluriannual forage crops (lucernes, clovers, grasses,…) that are mown 1-5 times per year. We conducted an experiment to test for possible interactions between the effects of cutting and competition on weed growth. Twelve annual weed species were grown under two levels of competition (presence or absence of lucerne) and with or without an early cutting treatment (2x2 factorial design). Both treatments had negative effects. When cutting and high competition were combined, all species produced lowest amounts of biomass. Our results suggest that both effects were purely additive for most of the species (neither compensation nor disproportionate amplification of the effects). This knowledge will be useful for designing innovative cropping systems combining productivity and sustainability.

Key words: Regrowth, Mowing, Temporary Grasslands, Integrated Weed Control.

LES EFFETS DE LA FAUCHE ET DE LA COMPETITION SUR LA CROISSANCE DES ADVENTICES : SONT-ILS ADDITIFS OU INTERACTIFS ?

RÉSUMÉ :

La croissance des adventices peut être affectée par des perturbations et par la compétition. Ces deux processus opposés sont importants dans des prairies temporaires (cultures fourragères pluriannuelles fauchées 1-5 fois par an). Une expérimentation a été réalisée pour tester les interactions entre ces deux processus. Douze espèces annuelles ont été cultivées

dans des conditions de compétition contrastées (présence ou absence de luzerne) et avec ou sans fauche précoce (dispositif factoriel 2x2). La production de biomasse par plante a été affectée par la fauche et par la compétition, et la combinaison des deux traitements a montré un effet purement additif pour la plupart des espèces (ni affaiblissement, ni renforcement disproportionnée des effets). Ces connaissances peuvent être utilisées pour concevoir des systèmes de culture conciliant productivité et durabilité.

Mots-clés : Croissance post-fauche, Compétition, Prairies temporaires, Gestion Intégrée.

INTRODUCTION

Plant fitness may be reduced by physical *disturbances* destroying parts of the plant's biomass, *competition* for resources by neighbouring plants, and different *stresses* as defined by Grime (1974). Therefore, plant population dynamics and communities may be structured by these three processes. Physical disturbances may have various origins such as abiotic factors (fire, frost, drought, inundation), biotic factors (herbivory, parasitism, grazing) or human factors such as agricultural management (harvesting, mowing, soil tillage). In arable fields, competition is the most important interaction between the cultivated crops and the spontaneously growing weeds (Zimdahl, 2004): crop yield may be reduced by competitive weeds and weed growth may be limited by competitive crops. On the other hand, disturbances created by different kinds of field operations will affect the plants and are used to suppress weeds.

Habitats are frequently distinguished by a dichotomy opposing competition and disturbance: Competition is lower in frequently disturbed habitats and higher in undisturbed habitats (Grime, 1974). However, both processes may also act in quick succession during the same vegetation period, for example in *perennial forage crops* (lucernes, clovers, grasses) sometimes called 'temporary grasslands'. In contrast to the classical annual crops that precede and follow them in long crop rotations, perennial crops remain in the field for about 2-6 years. Forage crops are mown 1-5 times per year for hay production creating disturbances. After each cutting, they show quick regrowth leading to high levels of competition during the whole vegetation period (except directly after mowing).

Perennial forage crops may have strong impacts on weed abundances and community composition, as suggested by a survey of farmers (Entz *et al.*, 1995), field observations (Ominski *et al.*, 1999), field experiments (Schoofs and Entz, 2000; Heggenstaller and Liebman, 2006) and seed bank studies (Clay and Aguilar, 1998; Sjursen, 2001; Bellinder *et al.*, 2004; Teasdale *et al.*, 2004; Albrecht, 2005). Most of these studies report reduced abundances of several problematic weed species after the cultivation of perennial crops, which would be beneficial for the following crops, while other species may profit from this crop type. Nevertheless, little is known about the *mechanisms* causing these effects.

Various *factors* may govern the plant's ability to survive and grow after cuttings or other physical disturbances destroying large parts of the aboveground biomass. These include i) the amount of green surface remaining after the disturbance for photosynthesis, ii) the presence of intact buds (apical meristems) needed for resprouting and iii) the quantity of C and N resources that can be remobilized for regrowth (reviewed in Meiss *et al.*, 2008).

These three factors may be affected by different *underlying variables* such as (a) the species functional group (annuals *vs.* perennials, grasses *vs.* broadleaved species,…) and (b) the plant size (biomass), (c) morphology and (d) age (phenological stage) as well as (e) cutting height, (f) date and (g) frequency (see references in Meiss *et al.*, 2008). Nevertheless, the plant regrowth capacity may also depend on general growth conditions (temperature, pH,…) and availability of growth resources (light, water, nutrients) depending on (ii) other farming operations, (ii) edaphic and climatic variables (soil type, nutrients, precipitation,

irradiation,…), and (ii) biotic interactions such as parasitism (diseases), symbioses and competition: a plant surviving a cutting treatment in 'optimal conditions' may show a reduced regrowth rate or even die in suboptimal conditions. In the present study, we focus on competition, which is of particular importance in temporary grasslands, pastures or field margin strips, which may all contain highly competitive perennial species (Schoofs and Entz, 2000; Dear *et al.*, 2006).

When acting separately, competition and physical disturbances will likely both have negative effects on plant fitness. When acting together, both processes may interact. These interactions may be considered from two directions, each with several mechanisms that may act simultaneously:

1) **Physical disturbances may change the actual community composition** and thus the *outcome of competition* (Weigelt and Jolliffe, 2003) through three mechanisms:

   a) creating "open" habitats by destroying disproportionate parts of the species actually dominating the community [generally the *competitive*, K-selected species (Pianka, 1970)], thus giving a "chance" to other species,

   b) favouring species that are not or are less affected by the specific type of disturbance due to special morphological or phenological traits (*resistant* species), or

   c) favouring species that can grow quickly after the disturbance [*resilient* or *opportunistic*, r-selected species (Pianka, 1970)].

2) **Competition may change the impact of the physical disturbance**

   a) by modifying the plant's morphology (height, specific leaf area,…) and phenology (stage) *before* the disturbance event: Mowing at a given height removes more biomass and buds from tall plants that were etiolated owing to competition compared to short plants grown in less competitive environments (Ballare and Casal, 2000).

   b) by modifying the performance of the damaged plants *after* the disturbance event. The likelihood of plant survival and the regrowth speed will thus probably decrease with increasing competition *after* the disturbance. The level of competition afterwards depends on the survival and regrowth of the neighbouring plants (forage crop). Due to the asymmetric nature of competition for light (Weiner and Damgaard, 2006), small differences in the regrowth speed between different species may have a big influence on the outcome of competition.

The possible effect (or sign) of such interactions on plant fitness may lie on a gradient between a positive interaction (disproportionate enhancement of the effects) and a strict negative interaction (compensation of negative effects) defined in Fig. 1.

In the cases A, B, and C of Fig. 1, the negative effect of one treatment is (more or less) *enhanced* by the addition of the other treatment. This may arise when competition before and/or after the cutting treatment increases the impact of cutting (mechanisms 2a and 2b). In contrast, the mechanisms 1a, 1b, and 1c might lead to all four cases defined in Fig. 1: If the strong repressive effect of the dominant species is broken by the cutting treatment, other species (weeds) may have a chance to establish, which would lead to a strict negative interaction (case D of Fig. 1). This corresponds to the 'classical view' founded by Grime (1974) that *opposes* disturbances and competition ('competitive' *vs.* 'disturbed habitats' or 'competitive' *vs.* 'ruderal species'. But if the actually dominant species (forage crop) has also the best regrowth ability (resilience) after cutting, its competitive advantage might also be *increased* by the disturbance, which would lead to cases A, B or C of Fig. 1.

Fig. 1: Illustration of possible interactions between the (negative) effects of cutting and competition on total biomass production of a weed plant. White boxes correspond to the reference (Ref.): biomass production of uncut plants with low competition. Striped boxes represent the cut plants, grey boxes plants experiencing stronger competition (comp.), grey striped boxes the combination of both treatments.

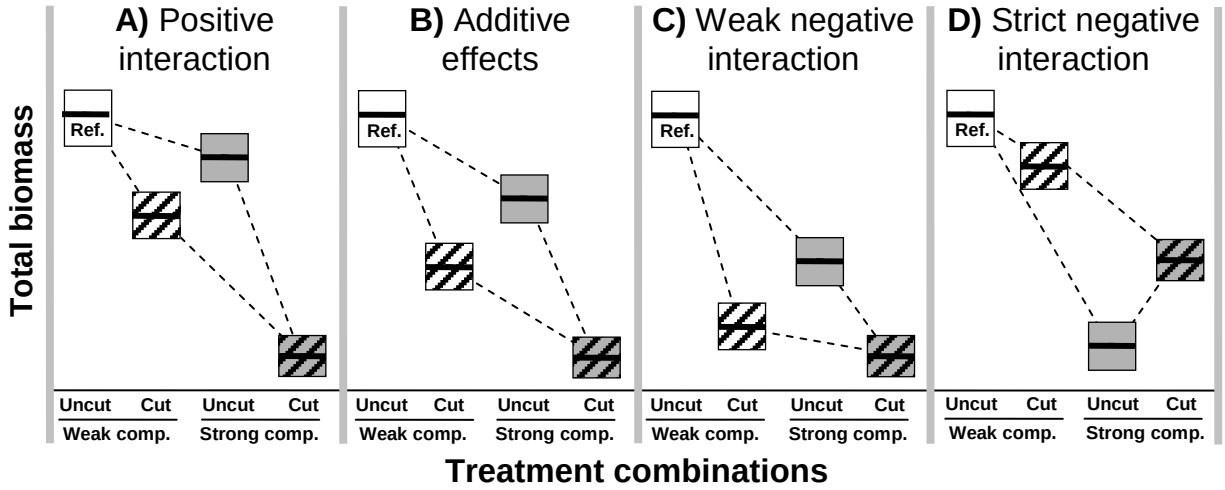
A) A *positive* interaction arises when the (negative) effect of one treatment is *disproportionally increased* by the other treatment. In this case, the combined effect of both treatments is *stronger* than expected by the sum of the effects of the separate treatments.

B) When combining both treatments, the two negative effects are simply *added* up. Additive effects are thus indicated by the parallelism of the dotted lines.

C) A *weak negative* interaction arises when the combined effect of both treatments is *weaker* than expected by the sum of the effects of both separate treatments.

D) A *strict negative* interaction arises when the strong effect of one treatment (here: competition) is *alleviated* by the other treatment (cutting).

***Fig. 1**: Illustration des interactions possibles entre les effets de la fauche et la compétition.*



In this paper, we investigate the possible interactions between cutting and competition on the plant growth of several annual weed species. We do not know about any study explicitly studying the interactions between both effects on weed plants, except Graglia *et al.* (2006), who analyzed the combined effects of mowing and competition on the biomass production of the perennial *Crisium arvense* in the following crop. Data on the performance of *annual* weeds are completely lacking. We thus study an open question and do not have any *a priori* expectations concerning the *sign* of the interaction. Using a full factorial design, we will analyze the effects of cutting and competition alone and in combination.

MATERIAL AND METHODS

The interaction between cutting and competition was studied using 12 annual weed species (Table I). Seeds were purchased from Herbiseed (www.herbiseed.com). Plants were grown in 8 experimental trays (57*37*15cm) containing a mixture of ¼ potting soil, ¼ field soil, ¼ turf, and ¼ vermiculite. Each tray was divided into 4 parts, each with 12 precise positions for weed plants. The 12 weed species were randomly allocated to these positions. After sowing (17 Dec 2007, 2-3 seeds per position), seeds were stratified for 3 weeks in darkness at 4°C to break seed dormancy of some weed species (Milberg and Andersson, 1998). Trays were then put into a greenhouse (5-17°C), regularly watered using an automatic system and fertilized when needed. Seedlings were thinned to one plant per position. Trays were put outside the greenhouse on 9 May 2008.

Table I: Species included in the experiment.
Table I: *Espèces inclus dans l'expérimentation.*

Scientific name	Code	An.	French	English
Adonis aestivalis L.	ADOAE		Adonis d'été	Pheasants-eye
Alopecurus myosuroides Huds.	ALOMY	x	Vulpin des champs	Blackgrass
Amaranthus retroflexus L.	AMARE		Amarante réfléchie	Common amaranth
Ambrosia artemisiifolia L.	AMBEL		Ambroisie	Common ragweed
Bromus sterilis L.	BROST	x	Brome stérile	Barren brome
Capsella bursa-pastoris Medi	CAPBP		Bourse à pasteur	Shepherd's-purse
Centaurea cyanus	CENCY		Bleuet des champs	Common cornflower
Chenopodium album L.	CHEAL	x	Chénopode blanc	Fat hen
Galium aparine L.	GALAP	x	Gaillet gratteron	Cleavers
Geranium dissectum L.	GERDI	x	Géranium découpé	Cut-leaved crane's-bill
Stellaria media (L.) Vill.	STEME		Mouron des oiseaux	Common chickweed
Veronica persica L.	VERPE	x	Véronique de perse	Field-speedwell
Medicago sativa L.	MEDSA		Luzerne cultivée	Alfalfa / Lucerne

An.: weed species used for interaction analysis.

We compared 4 experimental treatments by combining a competition and a cutting factor, each with two levels (see below). Each modality was represented by two separate trays and 4 target weed plants per species per tray (n=384 weed plants).

High and low **competition** levels were created by sowing lucerne plants in alternate rows at a high density (>70 plants/tray) all around the weed plants in half of the trays, the other half contained only weeds. Lucerne was chosen because it is known to have good regrowth ability (Meiss *et al.*, 2008) and to be highly competitive against weeds (Gosse *et al.*, 1988; Smith *et al.*, 1989; Schoofs and Entz, 2000; Meiss *et al.*, 2008).

For the **cutting** treatment, half of the trays were cut at an early date (25 March 2008), the other half was left uncut until the first common cutting date (16 April). Each weed and lucerne plant was cut separately at ~5cm from the soil surface using scissors. Plants with a creeping morphology were lifted up and cut at 5 cm from the rooting point. To study the long-term effects of cutting and competition on weed plants, trays were cut every 3-4 weeks from April until December 2008 (see Fig 3 for cutting dates).

DATA COLLECTION AND STATISTICAL ANALYSIS

We evaluated the aboveground plant biomass at each cutting date. The cut shoots of each individual weed plant were dried at 80°C for 48h and weighted. Lucerne dry weight was not evaluated at individual plant level but for the whole trays.

The interaction between the early cutting and competition treatments was analyzed comparing the biomass production per weed plant (cumulated up to the first common cutting date, 16 April). We present only the biomass data for 6 weed species (Table I) that had the most replicate plants to maximize statistical power. For the other weed species, numbers of individuals were too low, which was either caused by low germination or high mortality rates. Biomass data was log-transformed which improved normality and homoscedasticity of error variance (graphical verification using diagnostic plots of error distributions).

We first used a global model including all 6 weed species (3-way ANOVA). As we found significant interactions ($p<0.05$) between the species and both experimental treatments (Table II), we also calculated separate 2-way ANOVAs for each species. The treatment effects and interactions were illustrated using separate box-plots for each species. Single-

factor ANOVAs followed by Tukey tests were finally used to analyze the pairwise differences between the four treatments. Statistical tests and graphs were done using Systat 11 (Systat Software Inc.) and R 2.8.1 (R Development Core Team, 2008).

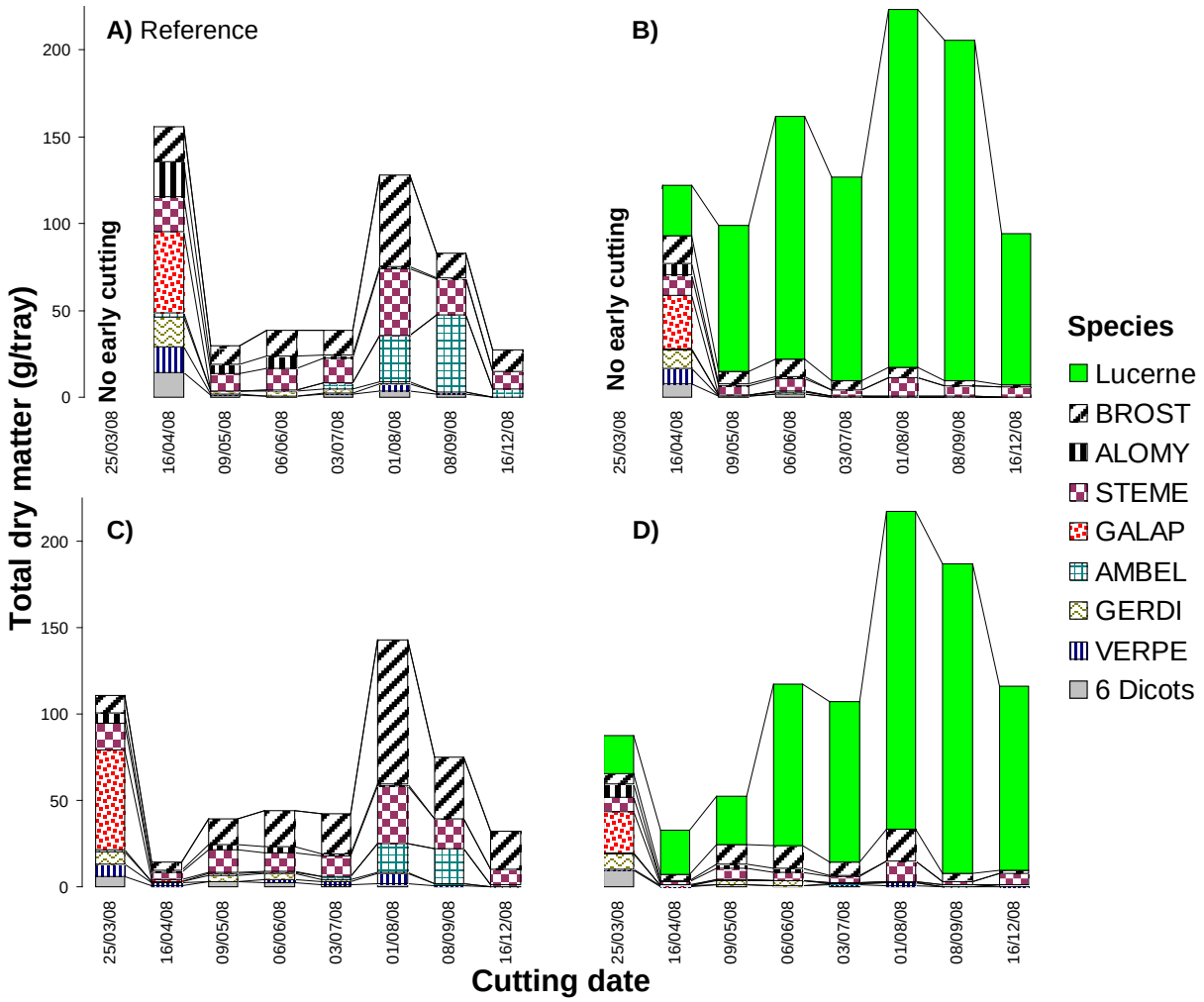
RESULTS

Biomass production varied strongly between the weed species ($p<0.0001$) explaining the largest amount of variance (Table II). Initial biomass production (prior to the first cut) was highest for *G. aparine* followed by *S. media*, *G. dissectum*, *B. sterilis*, *A. myosuroides*, *V. persica* and *C. album* (Fig. 2). Regrowth after the first cut was much lower than the biomass produced by initial growth. This was the case for all weed species in all treatments, but the contrary was observed for lucerne (Fig. 2). Nearly all individuals of *A. retroflexus* and *C. album* died already after the first (early or common) cutting treatment; some *G. aparine* plants survived the early cutting treatment but all died after the first common cutting. All other species survived longer, but only *B. sterilis*, *S. media* and *A. artemisiifolia* yielded significant amounts of biomass, especially in the trays without lucerne (Fig. 2).

Fig. 2 also illustrates the increasing impact of competition with time, caused by increasing lucerne biomass regrown after the successive cuttings. All species suffered from this competition, especially *B. sterilis*, *S. media*, *V. persica* and *A. artemisiifolia* (Fig. 2). In contrast, the initially strong impact of the additional early cutting treatment (causing the death of many weed plants) decreased during the consecutive cuttings, which were the same for all trays (Fig. 2). Therefore, the impact of differential cutting and interactions with competition are analyzed using the data of the first cutting dates (see Methods).

Fig. 2: Mean biomass (harvestable dry matter, cut at 5 cm above soil surface) of 12 weed species and lucerne cut at 8 consecutive dates for 4 treatments: **A)** Reference with no early cutting and low competition. **B)** No early cutting as A, but with higher competition (presence of lucerne). **C)** Low competition as A, but with an additional early cutting (25 March 2008). **D)** Combining high competition and early cutting treatments. See Table I for species codes. Grey bars indicate the biomass of other minor dicotyledonous weed species.

Fig. 2: *Biomasse moyenne de 12 espèces adventices + luzerne coupé à 8 dates consécutives pour 4 conditions expérimentales.*



When looking at the cumulative biomass production per plant up to the first common cutting treatment, the *reference plants* (no early cutting, low competition) of each species always had the highest biomasses (Fig. 3). *Cutting* always had a negative impact on biomass production, as (even) the sums of the cut + regrown biomasses were lower compared to the uncut reference plants. The effect of cutting was highly significant ($p<0.0001$) in the global model (Table II) and in 4 out of the 6 models for individual weed species (see Fig. 3 for details). Higher *competition* (presence of lucerne) also had a negative effect on weed biomass production, but weaker than the effect of cutting (at this early stage). The impact of competition was highly significant ($p=0.0002$) in the global model (Table II) but only in 2 out of the 6 models for individual weed species (Fig. 3).

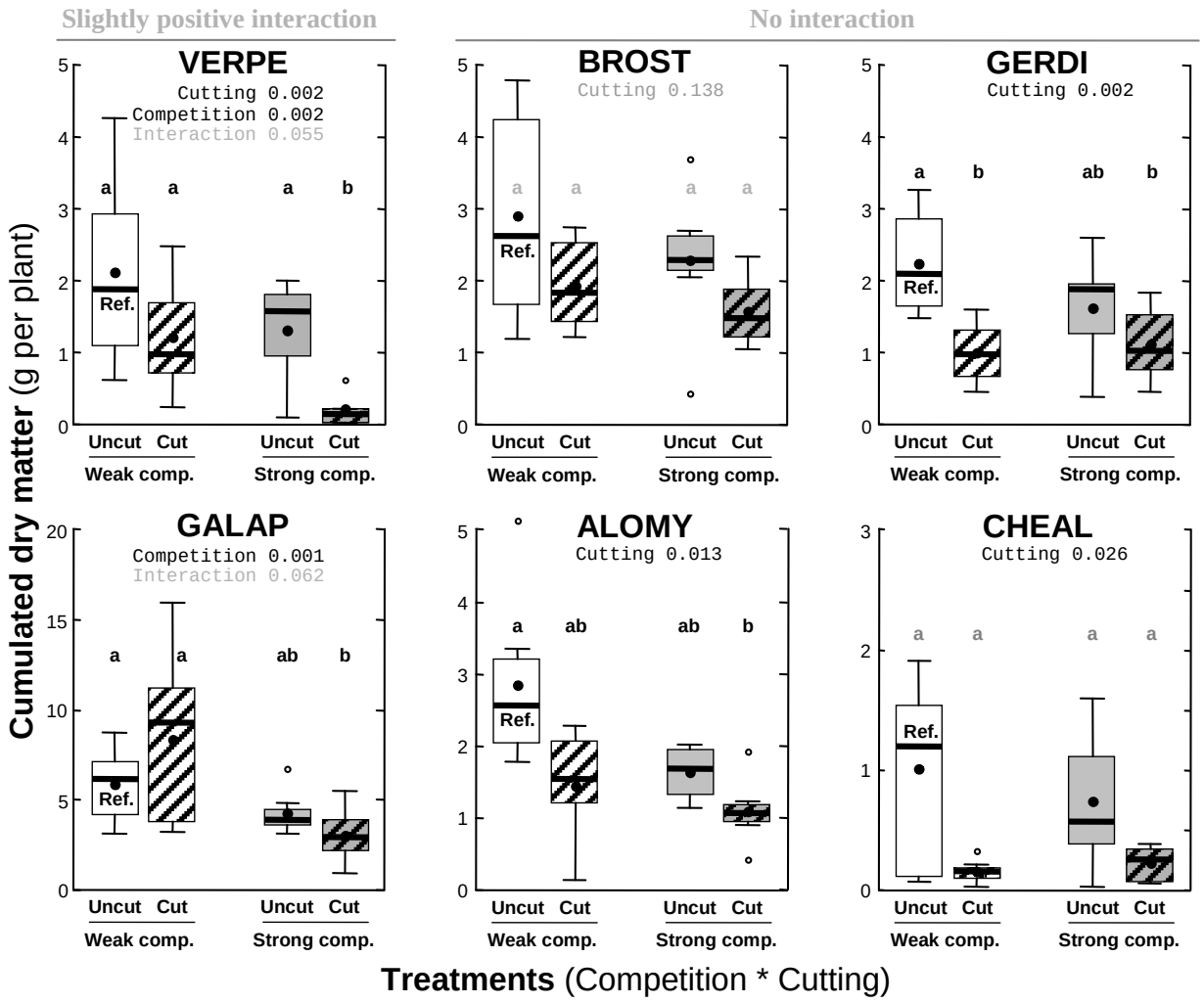
Source	SS	df	F	p
Model	31.68	23	14.2	**<.0001 ******
Error	13.59	140		
Weed species	23.34	5	48.1	**<.0001 ******
Competition	1.41	1	14.5	**0.0002 *****
Cutting	3.58	1	36.9	**<.0001 ******
Species*Cutting	1.49	5	3.1	**0.0116 ***
Species*Comp.	1.39	5	2.9	**0.0168 ***
Cutting*Comp.	0.01	1	0.1	0.7730 ns.
Species*Comp.*Cutting	1.12	5	2.3	**0.0476 ***

Table II: Three-way ANOVAs explaining the cumulated biomass per plant (log).

Table II: *ANOVA à trois facteurs expliquant la biomasse cumulée par*

Fig. 3: Cumulated biomass production per plant (sum of dry matter cut at early cutting + first common cutting) of 6 weed species in 4 experimental conditions as in Fig. 1. See Table I for species codes. Broad lines are median values, black dots mean values, boxes ranges between 25%- and 75%-quartiles (inter-quartile range), whiskers the last data point within 1.5 inter-quartile ranges, open circles further outliers. Significant effects of cutting, competition, and interactions are given below the species codes (p-values in 2-way ANOVAS). Treatments not connected by the same letter are significantly different at p=0.05 (Tukey).

Fig. 3: *Biomasse par plante de 6 espèces adventices dans 4 conditions expérimentales.*



When both treatments were *combined*, weed biomass production was lowest and plant mortality was highest compared to all other treatments (Fig. 2 and Fig. 3). In the global ANOVA model pooling all weed species, the *interaction* between cutting and competition was not significant but there was a slightly significant 3-way interaction (p=0.0476, Table II) indicating that the species reacted differently. When analyzing each species separately, the interaction term was nearly significant for *V. persica* (p=0.055) and *G. aparine* (p=0.062). For these two species, the interaction tended to be positive as the combination of cutting and competition produced plants that were rather smaller than expected supposing only additive effects (Fig. 3). The interaction term was not significant for the 4 other species. For *C. album*, the cutting treatment alone reduced biomass production very strongly so that the increased competition could not reduce plant growth any further (Fig. 3).

DISCUSSION

As expected from the literature (Andreasen *et al.*, 2002; Graglia *et al.*, 2006; Mager *et al.*, 2006) and our previous experiments (Meiss *et al.*, 2008), cumulated weed biomass production was reduced by cutting. In Fig. 3, we compared the biomass of uncut plants with the cumulated biomass production of cut plants (summing up the cut and the regrown dry matter). When considering only the biomass regrown, the impact of cutting was even stronger (Fig. 2).

Increased competition also had a negative effect on weed biomass production, but the amplitude of this effect was rather small at the beginning of the experiment, probably caused by the slow initial development the lucerne plants. Competition became more and more important as lucerne regrowth increased with the consecutive cuttings.

The combination of both treatments resulted in the lowest weed biomasses. The non-significant interaction terms and the graphical analysis (Fig. 3) suggest that the negative effects of both treatments are mainly additive. These results are in accordance with Graglia *et al.* (2006) who did not find any interaction between the negative effects of competition by grasses or clovers and the number of mowings on *C. arvense* biomass production in the following crop. For the two weed species where we observed a nearly significant interaction term (*V. persica* and *G. aparine*), the interaction tended to be *positive* (Fig. 3). There was thus no evidence that one treatment is counteracting or compensating the negative effect of the other treatment at this stage, but rather a tendency towards a mutual amplification.

Even though each cutting definitely reduced competition by removing the biggest part of the aboveground biomass, lucerne showed a good regrowth capacity rapidly restoring strong levels of competition after the disturbance events. Nevertheless, lucerne growth was also slightly affected by the additional early cutting treatment and produced slightly less biomass than the lucerne trays without the early cut. This lower lucerne biomass was probably the reason for slightly (but not significantly) higher weed biomass in the combined treatment compared to competition alone (compare Fig. 2D & 2B). This may be called an ‘indirect impact’ of the early cutting treatment. When lucerne is cut too early or too often, its regrowth ability may be reduced (Teixeira *et al.*, 2007) which may lead to reduced competition and thus a ‘strict negative interaction’ between cutting and competition.

Lucerne was already becoming the dominant species after the first cutting. It may thus be considered a ‘key stone species’ of the experimental system. Before the first cutting, total weed biomass was higher than lucerne biomass. The lucerne’s competitive advantage thus appears only after the cutting treatment. Without this disturbance, the lucerne would probably become the dominant species later. All 12 weed species showed less regrowth capacity than lucerne (Fig. 2). This corresponds to our previous experiments on plants grown in individual pots without competition (Meiss *et al.*, 2008). The present results show that (low) competition between different weed species and (higher) competition with additional lucerne plants will

increase the impact of cutting by further reducing the weed biomass production and the probability of surviving subsequent cuttings.

Besides negative effects of cutting and competition on biomass production, both processes might also delay or accelerate the phenological development of the weed plants, which would alter their reproductive output and their chance of surviving subsequent cuttings. The analysis of plant survivorship under the four treatments (data not shown) indicates that the plants in higher competition died earlier than the plants in low competition and that the plants not cut at the early date survived the longest in the case of all species except *Adonis aestivalis*, where cut plants survived longer.

CONCLUSION

By comparing cut and uncut plants in more and less competitive environments, we detected negative effects of both factors on weed biomass production. Our results suggest that both negative effects will add up when the two factors are combined (case B of Fig. 1 is thus the most likely situation). This knowledge is important for weed management, as competition and disturbances are closely related in various situations. These include not only mown forage crops, but also mown set-aside and field margin strips, annual crops where in-row-mowing techniques are used for weed control (Donald, 2006) and even grazed pastures. The concepts and findings presented here might be used to construct a model predicting the impacts of cutting and competition on weed growth and to optimize the cutting dates for Integrated Weed Management. In this study, we concentrated on the possible interactions between disturbances and competition; future studies should also investigate possible interactions between competition, disturbance and other stresses perceived by the weed plants.

ACKNOWLEDGEMENTS

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REFERENCES

(at the end of the thesis).

C.IV WEED SEED PREDATION

C.IV.1 **Article 6:**

Alignier, A., Meiss, H., Petit, S. & Reboud, X. (2008)

Variation of post-dispersal weed seed predation according to weed species, space and time.

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Variation of post-dispersal weed seed predation according to weed species, space and time

Artspezifische, räumliche und zeitliche Variation bei der Prädation von Unkrautsamen

A. Alignier[1*], H. Meiss[2], S. Petit[2] & X. Reboud[2]
[1] INRA Toulouse, UMR 1201 Dynamique forestière dans l'Espace Rural, Chemin de Borderouge 31326 Castanet-Tolosan, France.
[2] INRA Dijon, UMR 1210 Biologie et Gestion des Adventices, 17 rue Sully 21000 Dijon, France.
* Corresponding author, Audrey.Alignier@toulouse.inra.fr

Summary

Post-dispersal seed predation is an important source of mortality in plant populations. If this phenomenon is better known in tropical and woody systems, information is lacking for weeds in French agrosystems. In this paper, we evaluated seed predation variability in an organic wheat field by conducting experiments on weed seed preference and on spatial and temporal variation in predation rates. Weed seed predation preferences followed a species rank: *Viola arvensis* = *Stellaria media* > *Alopecurus myosuroides* = *Chenopodium album* > *Sinapis arvensis* = *Anagallis arvensis* = *Galium aparine* >> Plastic globules (for control), with weekly mean predation rates between 19 and 84%. The experiment on spatial variation in seed predation did not reveal a field border edge effect on predation rate with *S. arvensis*. However, a strong temporal variability has been found within a single season. Simple seeds characteristics as well as meteorological conditions were not directly correlated to predation rates obtained. High predation rates observed here underline the potential importance of this phenomenon on weed population dynamics. A future challenge would be to quantify the impact of post-dispersal seed predation on weed communities in order to assess the potential of seed predation for biological weed management.

Key words: agro-ecology, field border, Integrated Weed Management, weed population dynamics

Zusammenfassung

Die Prädation von Samen nach deren Ausbreitung ist einer der wichtigsten Mortalitätsfaktoren von Pflanzenpopulationen. Abgesehen von einigen Kenntnissen dieses Phänomens in tropischen Ökosystemen und bei Bäumen ist es bisher nahezu unerforscht bei Unkräutern in Frankreich. In einem biologischen bewirtschafteten Weizenfeld wurde anhand eines experimentellen Ansatzes die räumliche und zeitliche Variation, sowie die relative Stärke der Samenprädation bei 7 weit verbreiteten Ackerunkräutern untersucht. Innerhalb von einer Woche wurden je nach Art 19–84% der Samen durch Tiere entfernt, wobei eine signifikante Art-Rangordnung beobachtet wurde: *Viola arvensis* = *Stellaria media* > *Alopecurus myosuroides* = *Chenopodium album* > *Sinapis arvensis* = *Anagallis arvensis* = *Galium aparine* >> Plastikkügelchen (zur Kontrolle). Die Prädationsrate zeigte starke räumliche und zeitliche Schwankungen, die allerdings nicht direkt mit der Distanz zum Feldrand oder mit meteorologischen Variablen korreliert waren. Die beobachteten hohen Samenverluste deuten darauf hin, wie wichtig die Samenprädation für verschiedene Unkrautpopulationen sein kann. Um dieses Potential besser für den integrierten Pflanzenschutz nutzten zu können, ist mehr theoretische and angewandte Forschung nötig.

Stichwörter: Ackerwildkraut, Agrarökologie, biologische Unkrautkontrolle, Feldrand, Integrierter Pflanzenschutz, Populatiosdynamik

1 Introduction

Seeds may be considered a crucial stage of the life cycle for annual plants, such as arable weeds (Cardina et al. 2002), as they ensure population persistence in time (seed banks) and space (dispersion) (Chambers and MacMahon 1994; Tooley and Brust 2002). Seed banks may be reduced due to unsuccessful germination, senescence, physical damage, disease or parasite attack and predation. As seeds contain relatively more nutrients than stems, leaves and roots, they are highly sought after by predators (Hulme 1998). Very diverse groups of animals are known to consume seeds including both vertebrates (i.e. birds and rodents) and invertebrates (i.e. slugs, ants and ground beetles) (e.g. Cardina et al. 1996; Zhang et al. 1997; Cromar et al. 1999).

As a direct consequence of predation, seeds number may strongly be reduced conducting to important negative impacts on plant demography. Marino et al. (2005) and Pullaro et al. (2006) showed that a post-dispersal seed loss rate of 25–50% per year may have drastic impact on weed population growth. Nevertheless, in some cases, seeds may also profit from being predated; they could successfully establish at favourable microsites if they are still viable after passing through digestive track or if they are only displaced and not ingested (i.e. secondary dispersal, see VanderWall et al. 2005).

Despite its potential high impacts on population demography for annual plants, seed predation is rarely investigated for arable weeds. As far as we know, there are virtually no studies on weed seed predation older than 15–20 years; most of the existing studies being recent (see Tab. 1 for literature examples). Nevertheless, published predation rates can be very important (see Tab. 1).

Therefore, seed predation is increasingly viewed as an important ecological process that could potentially be exploited to improve agricultural weed management strategies and reduce the reliance on herbicides (Marino et al. 1997; Westerman et al. 2003a; Holmes and FroudWilliams 2005). To use weed seed predation for these agro-environmental goals, information is needed about the factors shaping it. Many factors are supposed to affect predation intensity. These factors can be partitioned into few categories: those related 1) to predators such as the predatory species present and their abundances and activities (Holl and Lulow 1997; Westerman et al. 2003b), 2) to human controlled environmental factors like actual crop (Heggenstaller et al. 2006), crop management practices (Hatcher and Melander 2003; Menalled et al. 2006), field shape affecting distance to field border (Marino et al. 1997; Spafford Jacob 2006), 3) to weather variability and season's alternation (Honek et al. 2006) and 4) to innate

Tab. 1: Examples of studies investigating post-dispersal weed seed predation rates in arable fields.
Tab. 1: Beispiele von Studien zur Prädation von Unkrautsamen in Äckern.

Predation rates	Crop	Weed species studied	Period	Location	Reference
10–90%	Maize	*Digitaria sanguinalis* L. *Setaria faberii* Herrm. *Amaranthus retroflexus* L. *Abutilon theophrasti* Medicus	Aug-Sept	Michigan, USA	Menalled et al. 2000
32–68%	Maize, Soybean	*Abutilon theophrasti* Medic. *Setaria faberii* Herrm.	48 h	Iowa, USA	Heggenstaller et al. 2006
32–70%	Cereal	*Stellaria media* L. *Chenopodium album* L. *Avena fatua* L.	May-June	Netherlands	Westerman et al. 2003b
35–67%	Wheat	*Avena fatua* L. *Chenopodium album* L. *Cirsium arvense* L.	One year	England	Holmes and FroudWilliams 2005
40–66%	Wheat	Lolium rigidum Gaudin *Avena fatua* L. *Raphanus raphanistrum* L.	One year	Australia	Spafford Jacob et al. 2006
88%	Maize, Soybean	*Ambrosia trifida* L. *Abutilon theophrasti* Medik.	One year	Ohio, USA	Cardina et al. 2002
80–90%	Maize, Soybean	*Setaria faberii* Herrm.	Aug-Sept	Iowa, USA	O'Rourke et al. 2006

seed characteristics, including morphology, nutritional quality and abundance (Hulme 1997; Xiao et al. 2006).

Seed predators could affect plant community composition by modifying the competitive abilities of the component species through feeding preferences (Louda et al. 1990 in Cromar et al. 1999). However, most experimental evaluations investigating weed seed predation were only conducted on few species or only a single one (see Tab. 1), so species preferences can not be established.

Studies investigating the effect of distance to the field border on seed predation did not conduct to consistent results. Marino et al. (1997) found a patchy distribution of post-dispersal seed predation rates which was not consistently related to the relative distance of field margins. In contrast, Spafford Jacob (2006) showed a negative correlation between seed predation rates and distance from field edge.

In this paper, we report on three separate experiments designed to investigate the potential variability of post-dispersal weed seed predation in an organic wheat agrosystem. The aim was to determine: 1) the predation rate of 7 contrasted weed species in order to assess seed species preferences, 2) the spatial pattern of seed predation to investigate potential field border effect on seed predation rates and 3) the small scale temporal variability of weed seed predation within a single season.

2 Materials and methods

Experiments designed to assess seed preferences and the effect of the distance to the field border on predation was conducted in an organic winter wheat field located at Fénay in Burgundy (47.23° N 5.07° E). The investigated eastern border of the field was constituted by an herbaceous field margin followed by a farm track and a small fir wood (*Picea abies*). The experiment on temporal variability of predation was carried out in garden parcel situated in INRA Dijon (47.20° N 5.02° E).

Weed seed predation was measured using seed cards following the methodology developed by Westerman et al. (2003a). Predation rate was assessed by monitoring removal of 50 randomly scattered seeds, which were slightly glued on sandpaper cards (5 cm*10 cm, grain size 100). The glue (adhesive spray, Sader; Bostik SA, Paris, France) ensured that seeds were not accidentally lost due to wind or rain, while seed predators were still able to remove them. Nails were used to fix the cards to the ground. Westerman et al. (2003a) report that neither the sandpaper nor the glue caused attraction, avoidance or any behavioural disturbance to any of the seed predators.

Species choice was based on model species used in the laboratory. Seeds were obtained from Herbiseed, Twyford, Berkshire, UK (http://www.herbiseed.com). All seeds (~35000) used in the experiment were gamma-irradiated at 15 kGray in order to inhibit germination. Irradiation was considered as a good compromise between prevention of seed escape/germination and conservation of the nutritional quality of seeds.

Control cards covered by a cage made out of a narrow wire mesh (1 mm^2) were used to estimate the fraction of accidental seed loss (as a result of handling, weather and other ambient factor not related to aboveground predation) (Westerman et al. 2003a). At the end of each experiment, when approximately one half of the seeds had disappeared, seed cards were picked out of the soil and returned to the laboratory where they were counted.

Seed predation rates were quantified as the percentage loss on exposed cards relative to the number of seeds remaining on the covered control cards (Abbott 1945):

$$R = (C-E)/C$$

where R is the proportion of seeds removed by predators, E is the number of seeds remaining on exposed cards and C is the number of seeds remaining on control cards.

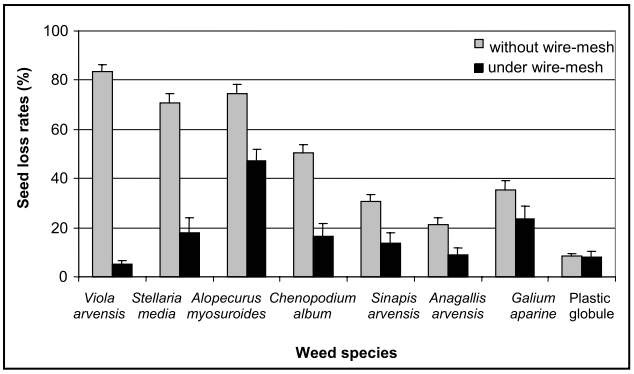

Fig. 1A: Seed losses rates (mean + SD) of seven weed species. For control predators are excluded by wire-mesh (1 mm²).

Abb. 1A: Samenverlustraten (Mittelwert + Stabw.) von sieben Unkrautarten und Plastikkugeln. In der Kontrollvariante wurden die Prädatoren mit einer Gitterabdeckung ausgeschlossen.

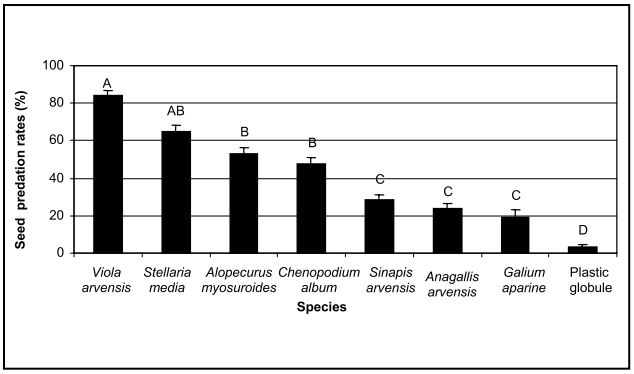

Fig. 1B: Seed predation rates (mean + SD) of seven weed species and artificial plastic globules. Corrected for seed losses under 1 mm-wire mesh (Abbott 1945). Means with different letters are statistically different at α=0.05.

Abb. 1B: Samenprädationsraten (Mittelwert + Stabw.) von sieben Unkrautarten und künstlichen Plastikkugeln. Korrigiert um die Samenverluste unter einer Gitterabdeckung (Abbott 1945).

2.1 Weed seed species preference

A total of seven annual weed species were selected, which presented diversity in terms of weight, morphology and nutritional value (see Tab. 2). To have a supplementary control, we added plastic globules as an unattractive artificial seed. Seeds cards were constituted by all 36 pairs of species (with 25 seeds per species = 50 seeds per card at total). Each of these 36 pairs was repeated on 15 cards to be exposed for predation. Two additional replicates of each pair were used as control cards covered by cages of wire mesh. Cards were placed on field for one week.

As the assumptions for one-way ANOVA could not be satisfied by simple data transformation, the predation rates *per* species were analyzed by the Kruskal-Wallis test and mean values were compared using the Mann-Whitney test with α=0.05. In addition, for each weed species, we looked at potential correlations between seed predation rates and three seed parameters i.e. their weight, lipid content and protein content (http://dijon.inra.fr/hyppa/hyppa-f.htm and http://rbgkew.org.uk/data/sid).

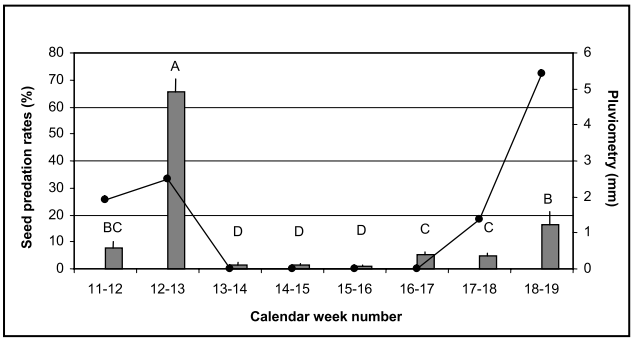

Fig. 2: Seed predation rates of Sinapis arvensis L. during eight weeks (from 21st March to 16th May 2007) and average pluviometry per week. Means with different letters are statistically different at α=0.05.

Abb. 2: Samenprädation bei Sinapis arvensis L. während acht Wochen (vom 21. März bis zum 16. Mai 2007) sowie die mittleren wöchentlichen Niederschläge dieses Zeitraumes.

2.2 Spatial pattern of weed seed predation

In this experiment, we placed 150 exposed and 20 control cards with 50 seeds of *Sinapis arvensis* L. (as found well-consumed by preliminary observation) along 17 replicate transects (separated by 10 m from each other) with 10 cards per transect. Transects ran perpendicularly to the field border and cards were placed at -6, -5, -1, 0, 1, 2, 4, 8, 16, 32 m distance from field edge (outside and within the field). The position of control cards along transect was randomised. As the removal rate of *S. arvensis* removal rate was lower than expected, the assay lasted 4 weeks in the field.

Agricultural activities during this experiment disrupted 12% of the seed cards. We therefore had to replace the values of the missing control cards by the global mean loss of the remaining control cards. Seed predation rates obtained were analysed using ANOVA. Effects of field border distance on seed predation rates were assessed with the non-parametric Spearman's correlation coefficient.

2.3 Temporal pattern of weed seed predation

To evaluate intra-seasonal patterns of seed predation, we measured rates of seed removal by predators during 8 successive one-week periods from March 21st to May 16th 2007. For each sampling period 15 exposed and 2 control cards with 50 seeds of *Sinapis arvensis* L. were pinned to the soil. Card location were randomized and always separated by at least 1m.

The weekly variability in seed predation rates was assessed by a Kruskal-Wallis test and mean values were separated using Mann-Whitney's test with α=0.05. The effect of temperature and precipitations were analyzed using a Spearman's correlation coefficient.

3 Results

3.1 Weed seed preference

Accidental seed removal from mesh-covered control cards was ~18 ± 5% (mean ± SD) on average and showed considerable variation between species ranging from 5% for *Viola arvensis* to 47%, for *Alopecurus myosuroides* (Fig. 1A).

Tab. 2: Characteristics for the seven weed seed species studied.
Tab. 2: Samengewicht, Fett- und Proteingehalt der Samen von sieben Unkrautarten.

Weed species	Thousand seed weight (g)	Lipid content (%)	Protein content (%)
Alopecurus myosuroides Huds.	1.9	19.0	20.1
Anagallis arvensis L.	0.5	19.2	14.8
Chenopodium album L	0.8	9.3	19.4
Galium aparine L.	9.0	3.1	12.7
Sinapis arvensis L.	2.4	29.2	28.8
Stellaria media L.	0.3	5.9	17.8
Viola arvensis Murray	0.4	*	*

Sources: http://www.dijon.inra.fr/hyppa/hyppa-f.htm and http://rbgkew.org.uk/data/sid.
* indicate missing data.

The global mean of seed predation rates corrected by seed removals on control cards (Abbott 1925) was about 40% during one week. Considerable differences were detected between the species (Wilcoxon test χ^2= 381.443 *df*=7 p<0.0001). Statistical analysis allowed establishing a species preference rank where seed predation was highest for *Viola arvensis* (84 ± 3%) (mean ± SD) and *Stellaria media* (65 ± 4%) and lowest for *Galium aparine* (19 ± 4%) (Fig. 1B). Seed predation rates were neither significantly correlated with seed weight ($\rho_{Spearman}$= -0.3923 p=0.383), nor with seed lipid content ($r_{Pearson}$ =0.138 p=0.767), nor with seed protein content ($r_{Pearson}$ = 0.572 p=0.179).

3.2 Spatial pattern of weed seed predation

After 4 weeks, 18 ± 2% (mean ± SD) of the seeds were removed. There were significant differences in seed predation rates between the locations ($F_{9,135}$=2.078 p=0.036). But no significant correlations were detected between predation rate and distance to the field margin ($\rho_{Spearman}$= -0.082 p=0.340). The highest predation rates occurred within the field at +8 m distance from the field margin (37±10%), the lowest rates at +4 m from the margin (7±7%). Moreover, there was no distinction between seed predation rates within and outside the field.

3.3 Temporal pattern of weed seed predation

Averaged over the season, seed loss was 13 ± 6% (mean ± SD). Weed seed predation rates varied significantly between the 8 weeks (Wilcoxon test χ^2=61.422 *df*=7 p<0.0001, Fig. 2). If there was no significant correlation between predation rates and weekly temperature ($\rho_{Spearman}$= -0.476 p=0.233), seed predation was positively correlated with weekly mean precipitation ($\rho_{Spearman}$= 0.849 p=0.007, Fig. 2) although this correlation explained 13% of observed variation of seed predation.

4 Discussion

We observed a strong preference rank between the 7 weed species studied. This ranking is in accordance with other published studies. For example, Westerman et al. (2003a) reported that predators prefer *V. arvensis* and *S. media* seeds more than *C. album*. Marshall et al. (2003) and Storkey (2006) stated that species such as *S. media* and *A. myosuroides* constitute more important food resources for birds and invertebrates in agrosystems than *Anagallis arvensis* for example.

Among seed characteristics likely to explain seed predation variability, seed size has often been cited (Hulme 1998). However, we could not detect such an effect in this study. The fact that no correlation was found between preferences and the three seed traits we investigated (thousand seed weight, lipid and protein content) suggests that other factors like toxins, or other attractive or repulsive secondary substances in the seeds could be more important (Kollman et al. 1998; Rey et al. 2002).

The high seed predation rates reported in this experiment (19 to 84% per week) highlight that some weed seeds may constitute an important food resource for animals living in agrosystems and may be an important factor shaping population dynamic and community composition of arable weeds. Specific differences observed in predation rates suggest that predation could contribute to increase the variations in species distribution. By modifying competitiveness via decreasing of seed density, seed predators can influence the composition and size of future weed populations (Cromar et al. 1999; Kollman and Bassin 2001). However, because we did not identify seed predators responsible for seed removals in our study, it is difficult to evaluate the influence of predators' preference on weed seed population dynamics. If seed predation is a key process during regeneration of plant populations, caution is needed when predicting demographic patterns only from short-term experiments.

In spite of the spatial variation of seed predation observed, our results did not confirm the hypothesis that predation is more important close to the field edge than in the field centre. Our results therefore comfort the view of Marino et al. (1997) that the field border effect reported by Spafford Jacob et al. (2006) cannot be generalised. This result could partly be explained by the fact that our study was conducted on an organic field without selective pressure of herbicide or insecticide. In addition, a transect of 38 m length may be sufficient for taking account for invertebrates activity, but it is relatively short compared with an average rodent home range, which may have up to 300 m of diameter (e.g. Szacki 1999 in Kollman and Buschor 2002). Kollman and Buschor (2002) demonstrate that edge effects *per se* are of little importance while factors such as vegetation cover, structure, density and management of edges maybe strongly influence the abundance and activities of more predators. Further research on field edge effect in seed predation should focus on the vegetation structure and composition of field edges.

Many studies have investigated the predation rates at different seasons of the year (Ji-Qi and Zhi-Bin 2004; Honek et al. 2006). However, little is known about the variation of

seed predation at finer temporal scales (*within* one season). Seasonal effect variations are supposed to be influenced by climatic variables such as temperature and rainfall. For example, the thermophilic nature of ants limits their spatial and temporal activity to relatively open microhabitats between April and September (Hulme 1997). In our study, predation rates varied considerably in time as could be expected, but this variation could not directly be explained by temperature, as already reported in other studies (Cardina et al. 2002). Seed predation rate was the highest during a week which was not the warmest. It is possible that relationship between predation rates and temperature was masked by the background seed availability. Indeed, if background seed availability is high, one might expect low predation on seed cards because there are alternative seed resources available (O'Rourke et al. 2006). We observed a slight but significant positive relation between weekly rainfall and seed predation rates. However, as we did not identify predators, we are not able to interpret this relation in terms of variation in the abundance or activity of seed predators. In conclusion, seed predation must be interpreted cautiously given the number of factors that are likely to influence interactions between seeds and predators.

In our study, predation appears to be a complex phenomenon, governed by numerous factors and interactions which vary both in space and time. Considering high seed predation rates observed in one week (40 % on average) predation thus could be a major ecological process able to affect weed population dynamics and possibly community composition *via* species. It would be interesting to examine the impacts of seed predation on weed communities, for example by exclusion experiments. Cromar et al. (1999) proposed that seed predation may be the most significant broad spectrum and natural form of biological weed control affecting the population dynamics of weeds. Implementing management practices that benefit seed predators, such as restricted use of pesticides or soil tillage, could enhance seed mortality and/or support other Integrated Weed Management strategies. To make optimal use of weed seed predation for reducing weeds infestation in arable farming, research should focus on the mechanisms causing variability in predation related to density/activity of seed predators.

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C.IV.2 **Article 7**:

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Bandes enherbées: Quelle flore, quelles prédateurs, quelle prédation?

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BANDES ENHERBEES : QUELLE FLORE, QUELS PREDATEURS, QUELLE PREDATION ?

S. Cordeau[1], H. Meiss[1,2], A. Boursault[1]
[1] INRA - UMR1210 INRA-ENESAD-UB Biologie et Gestion des Adventices.
17 rue Sully, BP 86510, 21065 Dijon cedex, France.
[2] Institute of Landscape Ecology and Resources Management, Division of Landscape Ecology and Landscape Planning, Justus-Liebig-University Giessen, Heinrich-Buff-Ring 26-32, D-35392 Giessen, Germany.
Email : stephane.cordeau@dijon.inra.fr

RESUME
Les bandes enherbées implantées pour des raisons environnementales le long des cours d'eau pourraient aussi faire office de réservoir de biodiversité végétale et animale. De plus, les adventices étant à la base des chaines trophiques, leurs graines constituent une nourriture non négligeable pour des oiseaux, des rongeurs et des invertébrés comme les carabiques. Ces organismes sont souvent abondants dans les agro-écosystèmes. Néanmoins, la prédation de graines dans les bandes enherbées est encore très mal connue. Par conséquent, connaissant de la flore adventice des bandes enherbées, quelle ressource en graines est potentiellement disponible pour les animaux ? Les bandes enherbées sont-elles un milieu riche en prédateurs de graines ? Quel taux de prédation peut-on y observer et varie t-il avec le mode gestion ? Nos résultats préliminaires montrent que les bandes enherbées sont un milieu riche en espèces adventices, dont les espèces les plus fréquentes sont vivaces. Les bandes non fauchées sont plus riches en adventices. Le taux de prédation de graines varie fortement entre les 7 espèces adventices testées (20-77%) mais aucune différence de prédation n'a été observée entre les zones fauchées et non-fauchées. Enfin la diversité des groupes de prédateurs est grande. Même si les agriculteurs ne souhaitent pas laisser grainer les adventices sur les bandes enherbées, la richesse floristique présente offre potentiellement beaucoup de nourriture aux animaux, notamment aux Carabidae. C'est donc un milieu, qui, de part la flore qui s'y développe, est potentiellement attractif pour l'entomofaune.
Mots clés : *bandes enherbées, adventices, graine, prédation, insecte, Carabidae.*

Title: Sown field margin strips: What flora, what seed predators, what weed seed predation?

ABSTRACT
Field margin strips sown alongside watercourses for environmental reasons may also constitute a refuge for plants and animals. Weed seeds may be important for the diets of birds, small mammals and various invertebrates, notably beetles. Such organisms may be abundant in agro-ecosystems, but weed seed predation has rarely been studied in field margin strips. Knowing the weed flora of the margin strips, what seed resources could be available for predators? Are sown field margin strips habitats with high seed predator abundances and diversities? What seed predation rates can be observed? Our preliminary results show that weed communities were very diverse and mostly characterized by perennial species. Uncut plots had higher plant species richness than cut plots. Seed predation rates varied strongly between 7 tested weed species (from 20 to 77% on average) but differences between cut and uncut plots were not significant. Seed predator diversities were high. Though most farmers don't like weed seed production on margin strips, the high floristic diversity on margin strips may offer a lot of food resources for farmland animals, especially beetles. Therefore, it can be an attractive habitat for weed seed predators.

Key words: *Field margin strips, weed, seed, predation, insect, Carabidae*

INTRODUCTION

Les agro-écosystèmes constituent actuellement le mode majoritaire d'usage des terres aux plans national et européen. De nombreux paysages gérés par l'homme contiennent une diversité spécifique comparable à celle de nombreux écosystèmes naturels (Altieri, 1999). Cependant, depuis la seconde moitié du vingtième siècle, l'intensification des modes de gestion des agro-écosystèmes sous l'influence de la Politique Agricole Commune (PAC) a entraîné une homogénéisation du paysage et la raréfaction ou l'extinction de nombreuses espèces de plantes, insectes, oiseaux et mammifères en France et en Europe (Benton *et al.*, 2003). Les agrosystèmes sont des systèmes caractérisés par des éléments paysagers en mosaïque. L'intensification agricole a aussi conduit à l'homogénéisation du paysage et résulte de l'augmentation de la taille des parcelles, de la destruction des haies, de la spécialisation de certaines régions de production mais également de la diminution des surfaces prairiales pérennes et temporaires. Or, à l'opposé des cultures annuelles dont la succession génère un environnement instable soumis à une forte variation des états du milieu, les milieux pérennes ont un rôle fonctionnel capital grâce à leur relative stabilité.

Or, depuis 2005, le paysage agricole français s'est doté d'un nouvel élément du paysage, stable dans le temps : les bandes enherbées. Sous l'impulsion de la réforme de la PAC de 2003 (mise en place du principe d'éco-conditionnalité des aides agricoles), les agriculteurs ont implanté ces « trames vertes » principalement le long des cours d'eau pour limiter la dérive des produits phytosanitaires et des fertilisants dans les eaux superficielles et limiter l'érosion hydrique des sols. Cette fonction environnementale a été très largement étudiée (Tollner *et al.*, 1976; Souiller *et al.*, 2002; Gry, 2006). Mais outre ce rôle premier, la mise en place de cette zone tampon dans le paysage agricole peut avoir des conséquences secondaires très diverses, tant agronomiques, écologiques, sociologiques que paysagères (Bernard *et al.*, 1998).
La réglementation impose qu'aucun produit phytosanitaire ni engrais chimique ou organique ne soit utilisé sur cette surface. De plus cet habitat est stable dans le temps, car les agriculteurs sèment la bande enherbée et ne travaille plus le sol comme ils le font dans la parcelle adjacente. Ainsi, ce milieu semi-naturel, à l'image des bords de champs ou des prairies, peut aussi faire office de réservoir de biodiversité végétale et animale (Benton *et al.*, 2003). Les bordures de champs sont des habitats connus pour cette fonction (Marshall and Moonen, 2002). Elles hébergent une flore riche et abondante (Fried *et al.*, 2009). La faune et l'entomofaune interagissent avec la flore en place. Cole *et al*. (2007) montrent qu'il existe un nombre d'espèces végétales plus important et un assemblage de carabiques différent dans les bandes enherbées gérées sans intervention que dans les bandes enherbées et les prairies gérées de manière intensive. Perner (2005) démontre que la composition des communautés de plantes affecte l'abondance des différents groupes fonctionnels d'arthropodes. Woodcock *et al.* (2007) trouvent que les groupes fonctionnels de scarabées peuvent être influencés par l'architecture de couvert végétal et sa composition. La diversité en arthropodes dans un habitat agricole semi-naturel est augmentée dans les bordures du champ en relation avec la diversité végétale (Thomas and Marshall, 1999).

De plus les espèces végétales présentes dans les bandes enherbées sont à la base de chaines trophiques. Les graines, notamment, constituent une nourriture non négligeable pour les oiseaux (Wilson *et al.*, 1999) (Blaney and Kotanen, 2001; Navntoft *et al.*, 2009), les rongeurs (Alcántara *et al.*, 2000) (Holmes and Froud-Williams, 2005) (Hulme, 1994; Hulme, 1998; Westerman *et al.*, 2003a; Westerman *et al.*, 2005) et les carabiques (Brust and House, 1988; Cromar *et al.*, 1999) (Honek *et al.*, 2003). Il est maintenant largement accepté que la prédation des graines d'adventices pourrait être une cause majeur de leur mortalité (Westerman *et al.*, 2003a; Westerman *et al.*, 2008) et qu'elle peut affecter toutes les espèces (Maron and Simms, 2001). L'impact de la prédation peut être particulièrement fort dans des cultures pérennes et les bandes enherbées, où l'ensemble des graines nouvellement

produites restent à la surface du sol contrairement aux cultures annuelles, où le sol est plus ou moins travaillé tous les ans.
De plus, les bandes enherbées sont un milieu riche en espèces végétales (Cordeau *et al.*, 2009b), et un réservoir potentiel d'adventices (Gardarin *et al.*, 2007b; Cordeau and Chauvel, 2009). Plusieurs études montrent que la prédation de graines varie en fonction de la densité du couvert végétal (Hulme, 1998; Gallandt *et al.*, 2005; Heggenstaller *et al.*, 2006). En effet, ces facteurs peuvent directement influencer les organismes prédateurs et leur habitat. Leur environnement immédiat détermine ainsi leur comportement de prédation (Manson and Stiles, 1998; Heggenstaller *et al.*, 2006). La nature du mélange semé et le type de gestion du couvert végétal (fauche) vont donc probablement influencer la prédation.

L'objectif de ce travail est de connaitre les espèces adventices se développant dans les bandes enherbées, illustrant la ressource potentielle de graines pour des prédateurs. Dans un autre temps, il s'agit de quantifier la prédation des graines d'adventices et d'identifier la présence d'insectes prédateurs. Quelle ressource en graines pourrait être disponible pour l'entomofaune ? Les bandes enherbées sont-elles un milieu riche en prédateurs de graines ? Quel taux de prédation peut-on y observer ? Ce taux de prédation varie t-il selon la gestion des bandes ou selon les espèces adventices ?

MATERIELS ET METHODES

Les bandes enherbées ont été semées au printemps 2006 avec un mélange graminées-légumineuses : 40% *Dactylis glomerata*, 40% *Festuca rubra*, 20% *Lotus corniculatus*. Elles ont été entretenues de manière identique jusqu'en juin 2008 à raison de 3 fauchages par an. En juin 2008, 2 modes de gestion on été réalisés : Fauchage (modalité F+), et non fauchage (modalité F-). Les suivis ont été faits sur 2 bandes «F+» et 1 bande «F-». Les bandes mesurent 25 m de long sur 5 m de large (largeur réglementaire).

Relevés floristiques

Des relevés floristiques ont été réalisés avant fauchage (mi-juin) et deux mois après (mi aout). Les 2 relevés de flore permettent d'observer la flore hivernale-printanière et la flore estivale. Par ailleurs, la description des espèces en présence a été faite sur le cumul des deux dates de relevés. La présence et l'abondance des espèces (semées ou adventices) a été notées. L'abondance est quantifiée par des pourcentages de recouvrement de chaque espèce selon l'échelle de Braun-Blanquet (Mueller-Dombois and Ellenberg, 1974) modifiée (5: l'espèce couvre plus de 75% du quadrat, 4 : entre 50 et 75%, 3 : entre 25 et 50%, 2 : entre 25 et 5%, 1 : <5 %, + : recouvrement insignifiant et r : un individu). L'abondance est quantifiée sur 4 quadrats de 0.36m² disposés par paire, soit 2 à un mètre de la culture et 2 à 1 mètre de la bordure herbacée. Pour compléter les relevés des quadrats, un parcours a été réalisé dans la bande permettant d'identifier les espèces présentes seulement en tâches. La nomenclature utilisée est la flore des champs cultivés (Jauzein, 1995). Une base de données composée à partir de la base de trait de vie BiolFlor (Kühn *et al.*, 2004) http://www.ufz.de/biolflor/index.jsp et de la flore des champs cultivés (Jauzein, 1995) a permis de caractériser les espèces rencontrées.

Mesure de la prédation

Nous avons utilisé la méthodologie « cartes à graines » développée par Westerman et *al*. (2003c) : 25 graines de chaque espèce sont fixées sur des cartes de papier de verre (5×10cm) à grains moyens (P 100) à l'aide d'une colle repositionnable (Sader ; Bostik SA, Paris, France). Le support et la colle choisis permettent une bonne tenue des graines sur la carte et une certaine résistance à la pluie et au vent, pour éviter des pertes accidentelles. Des clous assurent le bon maintien des cartes au sol. Sept espèces adventices ont été choisies : le chénopode blanc, *Chenopodium album* L. ; le gaillet grateron, *Galium aparine* L. ; la stellaire intermédiaire, *Stellaria media* (L.) Vill. ; le mouron de champs, *Anagallis arvensis* L. ; le vulpin des champs, *Alopecurus myosuroides* Huds. ; la moutarde des

champs, *Sinapis arvensis* L. ; la pensée des champs, *Viola arvensis* Murray. Ces espèces sont très communes dans les champs cultivés en France. Afin de quantifier les pertes accidentelles, des billes plastiques ont été disposées à coté des graines d'adventices. Les cartes ont été installées le 14 juillet. Après une période de 2 semaines d'exposition, les cartes ont été collectées et les graines restantes ont été comptées directement sur place. Le taux de prédation est calculé comme étant le pourcentage de graines enlevées durant la période. Aucune correction des taux de pertes de graines n'a été nécessaire vu les très faibles pertes accidentelles des billes plastiques.

Piégeage d'insectes

Le piégeage des insectes a été réalisé grâce à des pots pièges (diamètre = 7 cm, profondeur = 10 cm) contenant une solution alcoolique. Deux pots étaient disposés à environ 1m de chaque coté des 8 stations de cartes de prédation. Ils ont été mis en place un jour après les cartes et relevés une semaine après. Le contenu des pots a ensuite été trié par guilde et les coléoptères ont été identifiés à l'espèce à l'aide du guide des Coléoptères d'Europe (Du Chatenet, 2005).

Analyses statistiques

Concernant la flore, des tests t bilatéraux ont permis de comparer les moyennes des taux de recouvrement (totaux, espèces adventices et espèces semées) entre les modalités F+ et F-. Les taux de prédation et les abondances des carabiques ont été analysés tout d'abord par des ANOVA à deux facteurs : espèce (adventice ou carabique) et régime de fauche. En raison d'interactions significatives, des tests t bilatéraux ont ensuite été utilisés pour comparer les abondances des trois espèces carabiques principales dans les bandes F+ et F-

RESULTATS PRELIMINAIRES

Composition et structure des communautés végétales

Sur les bandes enherbées, 35 espèces adventices ont été recensées (Tableau 1) auxquelles s'ajoutent les 3 espèces semées. Dans les 2 bandes enherbées fauchées (F+), la richesse spécifique, observée dans les parcours, était de 22 espèces contre 24 dans la bande non fauchée (F-).

Parmi les 35 espèces, 65% sont pluriannuelles (Tableau 1). Selon Jauzein (1995), plus de 70% des espèces observées sont des espèces qualifiées de « très communes » à « assez communes », dans les parcelles agricoles, alors que seulement 9.7% sont « rares ». La couverture végétale totale des bandes était de 70.3 ± 15.1% (moyenne ± écart-type) pour les parties non fauchées (F-) et de 60.3 ± 18.6% pour les parties fauchées (F+). La différence n'est pas significative ($F_{1,22}$=1.687 ; p=0.207). Les espèces semées couvrent largement plus que les espèces adventices (Figure 1). Ainsi au sein des espèces semées comme des espèces adventices, le régime de fauche n'influe par sur le recouvrement des espèces.

Tableau 1 : Liste des espèces adventices rencontrées dans les bandes enherbées caractérisées par le type biologique (Raunkiær, 1905; BiolFlor Trait database, Kühn *et al.*, 2004), présence des espèces dans les bandes F+ et F- aux 2 dates de relevés, abondance moyenne (en pourcentage de recouvrement) sur les deux dates et fréquence d'observation moyenne sur les deux dates. Les espèces sont triées par leur fréquence d'observation.
Table 1 : *List of weed species in field margin strips with plant life forms (Raunkiær, 1905; BiolFlor Trait database, Kühn et al., 2004), occurrence of species in cut (F+) and uncut (F-) plots, mean abundance (in percentage of soil cover) and mean frequency of occurrence over both study dates. Species are sorted by the frequency of occurrence.*

Espèces	Type biologique	Présence dans les bandes F+	Présence dans les bandes F-	Abondance moyenne	Fréquence
Taraxacum officinale	Hemicryptophyte	1	1	1.12	100.0
Plantago lanceolata	Hemicryptophyte	1	1	0.44	41.7
Geranium dissectum	Therophyte	1	1	0.95	37.5
Cirsium arvense	Geophyte	1	1	0.21	25.0
Convolvulus arvensis	Geophyte	1	1	0.11	25.0
Daucus carota	Hemicryptophyte	1	1	0.21	25.0
Lolium sp.	Therophyte	1	1	0.13	25.0
Pastinaca sativa	Hemicryptophyte	1	1	0.64	20.8
Picris hieracioides	Hemicryptophyte	1	1	0.12	16.7
Potentilla repens	Hemicryptophyte	1	0	0.74	16.7
Sonchus asper	Therophyte	1	0	0.01	16.7
Trifolium sp.	non mentionné	1	1	0.11	16.7
Geranium rotundifolium	Therophyte	1	1	0.01	12.5
Verbena officinalis	Hemicryptophyte	1	0	<0.01	12.5
Veronica persica	Therophyte	1	1	0.11	12.5
Arctium lappa	Hemicryptophyte	1	0	2.19	8.3
Geranium colombinum	Therophyte	1	0	0.10	8.3
Geranium sp.	Therophyte	0	1	<0.01	8.3
Lamium purpureum	Therophyte	0	1	<0.01	8.3
Poa trivialis	Hemicryptophyte	0	1	<0.01	8.3
Rumex crispus	Hemicryptophyte	1	0	0.10	8.3
Silene latifolia subsp. alba	Hemicryptophyte	0	1	0.11	8.3
Tragopogon dubium	Hemicryptophyte	1	0	<0.01	8.3
Veronica arvensis	Therophyte	0	1	<0.01	8.3
Anagallis arvensis	Therophyte	0	1	0.10	4.2
Artemisia vulgaris	Hemicryptophyte	0	1	<0.01	4.2
Cerastium arvense	Hemicryptophyte	0	1	<0.01	4.2
Crepis vesicaria subsp. taraxacifolia	Hemicryptophyte	0	1	<0.01	4.2
Elytrigia repens	Geophyte	1	0	<0.01	4.2
Hypericum perforatum	Hemicryptophyte	0	1	0.63	4.2
Lactuca serriola	Therophyte	1	0	<0.01	4.2
Achillea millefolium	Hemicryptophyte	1	1	<0.01	0.0
Centaurea scabiosa	Hemicryptophyte	1	1	<0.01	0.0
Malva sylvestris	Hemicryptophyte	1	0	<0.01	0.0
Reseda lutea	Therophyte	1	1	<0.01	0.0

Prédation des graines d'adventices

Les pertes accidentelles de graines ont été très faibles (2.9% en moyenne pour les billes en plastique). Le taux de prédation de graines varie significativement en fonction de l'espèce adventice ($F_{6,42}$=3.47 ; p=0.007) entre 77% pour *Viola arvensis* et 20% pour *Galium aparine* (Figure 2). Mais aucune différence significative du taux de prédation n'a été observée entre les zones fauchées et non-fauchées ($F_{1,42}$=0.25 ; p=0.617) (46% contre 51% en moyenne). L'interaction entre l'entretien de bandes et les espèces adventices n'est pas significative ($F_{1,42}$=0.96 ; p=0.467).

Figure 1 : Recouvrement des espèces semées et adventices dans les bandes enherbées fauchées (F+) et non fauchées (F-). Les recouvrements non qualifiés par les mêmes lettres sont significativement différents (test de Tukey).
Figure 1: *Soil cover rates of sown and weed species in cut and uncut treatments (F+, F-). Rates not connected by the same letter are significantly different (Tukey).*

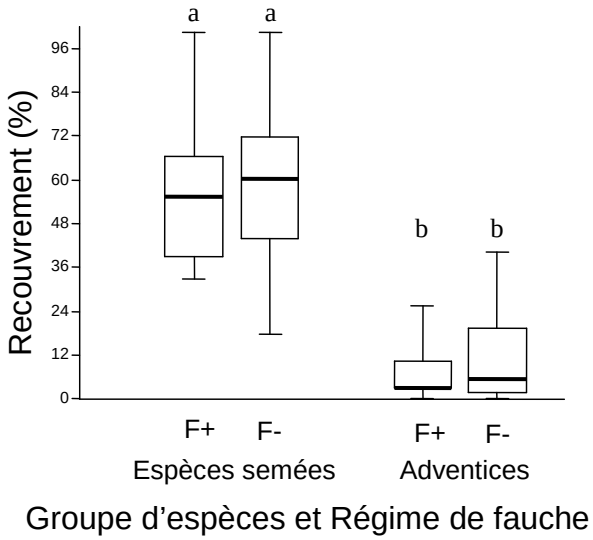
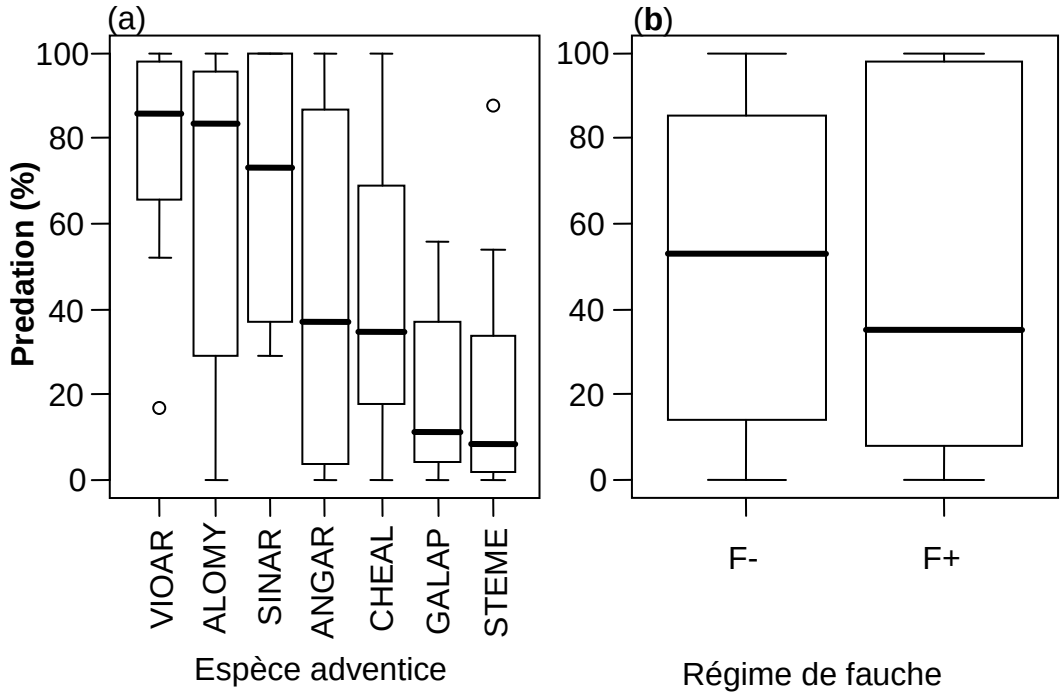


Figure 2 : Taux de prédation des graines d'adventices, (a) en fonction de l'espèce adventice et (b) du régime d'entretien. GALAP, *Galium aparine* ; STEME, *Stellaria media* ; CHEAL, *Chenopodium album* ; ANGAR, *Anagallis arvensis* ; ALOMY, *Alopecurus myosuroides* ; SINAR, *Sinapis arvensis* ; VIOAR, *Viola arvensis* ; F+, bande fauchée ; F-, bande non fauchée.
Figure 2 : *Weed seed predation rates (a) as a function of weed species and (b) cutting treatment. F+, cut; F-, uncut.*

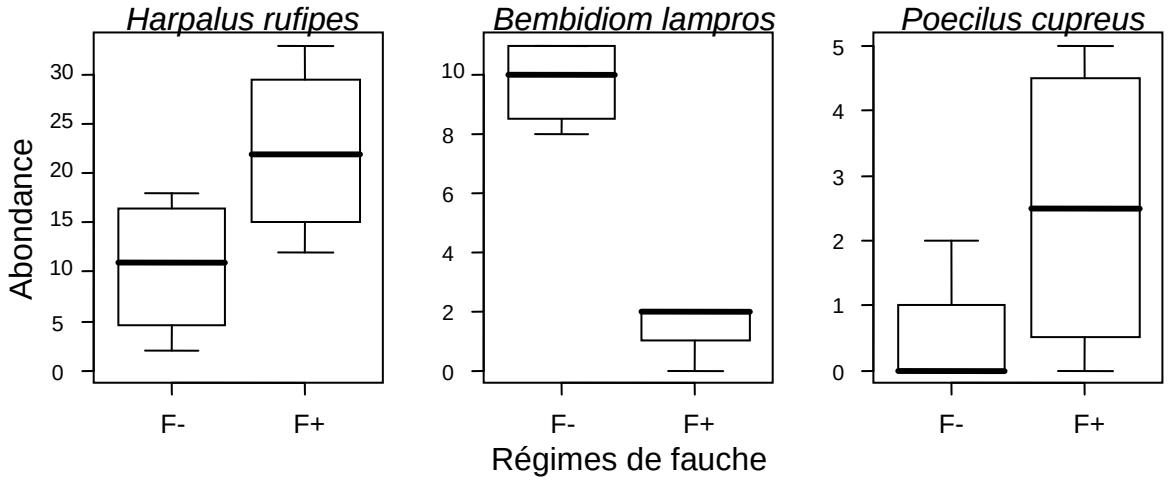


Insectes prédateurs

Les principaux invertébrés granivores piégés sont les carabiques. Au total, 113 individus de carabiques ont été piégés dans la bande F+ contre 85 dans la bande F-. L'analyse de variance a montré une forte interaction entre l'espèce de carabique et le régime de fauche ($F_{6,42}$=5.39 ; p=0.0003) (Figure 3). L'abondance de *Bembidiom lampros* était plus forte dans les bandes F- que dans F+ ($t_{1,3}$=5.5, p=0.0067). *Harpalus rufipes* et *Poecilus cupreus* ont montré des patterns inverses (Figure 3), mais les différences n'étaient pas significatives.

Figure 3 : Abondances (en nombre d'individus par piège) des trois espèces carabiques majoritaires. F+, bande fauchée ; F-, bande non fauchée.

Figure 3 : *Abundances (number of individuals per trap) of three main carabid species. F+, cut; F-, uncut field margin strips.*



La richesse spécifique était de 7 dans la bande F+ et de 4 dans la bande F-. Néanmoins, l'indice de Shannon est quelque peu supérieur dans la bande non fauchée (H' = 0.88) que dans la bande fauchée (H' = 0.84), ceci pouvant s'expliquer par la prédominance, dans cette dernière, d'*Harpalus rufipes* (Figure 3).

DISCUSSION

Le dispositif était de petite envergure. Afin d'éclaircir les résultats préliminaires il faudrait mettre en place une expérimentation permettant d'aboutir à un jeu de données plus important. Ainsi, il serait alors intéressant de regarder plus en détails les relations entre couverture végétale, richesse végétale, abondance des prédateurs et taux de prédation.

Cependant, cette analyse préliminaire permet de décrire trois aspects importants du fonctionnement de l'agro-écosystème : la fore adventice comme ressource trophique potentielle, la communauté de carabiques comme importants prédateurs de graines et le processus de prédation.

Flore étudiée

Les résultats montrent que les bandes enherbées sont un milieu favorable au développement des adventices. En effet, nous avons observé une diversité spécifique 2 à 3 fois plus importante que dans les parcelles cultivées (Gardarin *et al.*, 2007b; Fried *et al.*, 2009). Néanmoins, l'abondance (taux de recouvrement) des adventices était très faible par rapport à celles des espèces semées. La moitié de ces espèces sont annuelles donc fortement dépendant de la reproduction par les graines pour se maintenir dans le milieu.

Sur le pas de temps de l'expérimentation, aucune différence n'a été observé en terme de recouvrement d'adventices entre les bandes enherbées fauchées et non-fauchées.

Prédation

Le taux de prédation varie fortement en fonction des espèces adventices. De nombreuses études ont montrés de telles préférences (Honek *et al.*, 2003; Honek *et al.*, 2007; Saska *et al.*, 2008). De plus, dans une étude préalable sur les mêmes espèces, l'ordre de préférences a été assez bien conservé (Alignier *et al.*, 2008). Cependant, les déterminants de ces choix sont encore peu connus. Compte tenu de ces préférences, on peut penser que la prédation pourrait changer la composition de la communauté végétale. En effet, les forts taux de prédation pourraient défavoriser les adventices annuelles au profit des espèces pérennes (semées et adventices).

Des études préalables ont montrées que la prédation varie en fonction de la couverture de végétation (Gallandt *et al.*, 2005; Heggenstaller *et al.*, 2006). L'absence de différences de taux de prédation entre les bandes fauchées et non fauchées (Figure 2) pourrait donc être due aux faibles différences de recouvrement entre ces deux modalités (Figure 1).

En effet, la végétation repousse très vite. Les cartes de prédation ont été disposées 4 semaines après la fauche. Ainsi, l'habitat n'était probablement pas si différent pour des prédateurs malgré les taux de couvertures végétales différents.

Enfin, le dispositif a été mis en place 15 jours en Juillet or on sait par ailleurs que les périodes d'activité des prédateurs se succèdent au cours du temps et que les prédateurs actifs se déplacent dans la mosaïque paysagère au cours de la saison, en fonction des ressources.

Prédateurs

Les espèces carabiques n´ont pas les mêmes besoins en terme d´habitat. En effet, certaines espèces préfèrent plutôt des milieux secs avec une lumière directe tandis que d´autres des zones plus abritées et plus humides (Holland, 2002). Or, la fauche va perturber le milieu et créer des types d´habitats différents qui pourraient expliquer les différences de composition des communautés carabiques. *Bembidiom lampros* est connu pour préférer les milieux couverts et humides (Holland, 2002) ce qui pourrait expliquer son abondance plus forte dans les bandes non fauchées. *Poecilus cupreus*, en revanche, est souvent associe aux milieux plus ouverts et semble ici être plus présent dans les bandes fauchées. On sait aussi que d'autres espèces sont moins exigeantes et plus ubiquistes, ce qui pourrait être le cas d´*Harpalus rufipes.* Nos résultats préliminaires suggèrent que le régime de fauche pourrait être un élément important pour la composition des communautés de carabiques.

Limites et perspectives

Dans cette étude, les espèces choisies pour étudier la prédation ne sont pas présentes dans la flore exprimée de ces bandes enherbées, excepté *Anagallis arvensis*. Ainsi il est assez difficile de relier la flore présente à une ressource potentielle de graines pour en étudier la prédation. De plus, la prédation a été mesurée à l'aide de cartes à graines qui n'étaient pas protégées par des cages d'exclusion. Ainsi, la prédation mesurée est celle de l'ensemble de la faune (vertébrés et invertébrés). Les carabiques recensés dans les pots pièges ne représentent qu'une partie des prédateurs potentiels.

Ainsi pour confirmer les résultats préliminaires, un dispositif de plus grande envergure intégrant des répétitions spatiales et temporelles serait nécessaire.

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REFERENCES BIBLIOGRAPHIQUES

(à la fin de la thèse).

C.IV.3 **Article 8:**

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Weed seed predation increases with vegetation cover in perennial forage crops

Helmut Meiss[a,b,*], Lise Le Lagadec[a], Nicolas Munier-Jolain[a], Rainer Waldhardt[b], Sandrine Petit[a]

[a] INRA, UMR 1210 Biologie et Gestion des Adventices, F-21000 Dijon, France
[b] Institute of Landscape Ecology and Resources Management, Division of Landscape Ecology and Landscape Planning, Justus-Liebig-University Giessen, IFZ, Heinrich-Buff-Ring 26-32, D-35392 Giessen, Germany

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ABSTRACT

Vegetation cover may affect weed seed predation by modifying the habitat quality for predatory organisms. Post-dispersal weed seed predation was measured by placing 'seed cards' in two perennial crops (alfalfa, cocksfoot) with and without crop cutting and in plots with bare soil. Each treatment was repeated four times in a randomized complete block design. Vegetation cover was measured by canopy light interception. Predation trials lasted two weeks and were repeated three times. Seed predation rates varied among three weed species (highest for *Viola arvensis*, intermediate for *Alopecurus myosuroides*, lowest for *Sinapis arvensis*). Vertebrate exclusion cages (12 mm × 12 mm openings) strongly reduced seed predation rates. Positive relationships were observed between vegetation cover and seed predation rates by both vertebrates and invertebrates for all weed species and trials, except when overall predation rates were very low. Predation rates were highest in uncut alfalfa, lowest on bare soil, but 16–64% of this variation could equally be explained by vegetation cover. The factorial design indicated that cutting had a stronger impact than crop species (legume or grass). Results suggest that weed seed predation may be enhanced by maintaining a high and temporally extended vegetation cover.

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1. Introduction

Weed seed predation may be considered a valuable ecosystem service for two reasons. First, weed seeds constitute an important part of the diet of animals including various invertebrates, small mammals and birds (Manson and Stiles, 1998; Wilson et al., 1999; Kollmann and Bassin, 2001). The reduced availability of this food resource is probably a major cause of the biodiversity loss observed in farmed landscapes during recent decades (Robinson and Sutherland, 2002). Second, seed predation may reduce the density of weed populations. Both experiments (Menalled et al., 2000; Davis and Liebman, 2003; Westerman et al., 2003b; Mauchline et al., 2005) and modelling studies (Jordan et al., 1995; Davis et al., 2004; Kauffman and Maron, 2006) suggest that seed predation may have a very strong impact on weed population demography. Westerman et al. (2005) showed that seed loss rates exceeding 40% per year would be sufficient to stabilize *Abutilon theophrasti* Medik. population densities in a low-herbicide system. Promoting weed seed predation may thus (1) be beneficial to farmland biodiversity and (2) contribute to preventive weed management and hence decrease the need for curative weed control.

Among the multitude of factors that may influence seed predation, vegetation cover and crop species could play a key role, because they may affect the quality of the foraging habitat for seed predators. Several studies compared the weed seed predation rates and/or the abundances of seed predators in different crop species (Andersson, 1998; Zhang et al., 1998; Cromar et al., 1999; Kromp, 1999; Macdonald et al., 2000; Westerman et al., 2005; Menalled et al., 2006; O'Rourke et al., 2006, 2008). In contrast, few studies have dealt explicitly with the vegetation cover, they vary in scope, geographical location, habitat, seed and predator group, yet most of them have found its impact to be positive as shown in the literature review made in Table 1.

In the study of Heggenstaller et al. (2006) weed seed predation rates roughly paralleled the development of biomass during the growing season of annual crops as well as the periodic cutting and regrowth dynamic in mown perennial forage crops. However, disentangling seasonal effects (e.g., variations in predator abundance/activity) from vegetation cover effects would require comparing simultaneously situations of contrasting degrees of vegetation cover of the same crop species.

In this paper, we report experimental results where weed seed predation was measured in different perennial forage crops with and without crop cutting, where cut and uncut plots of each crop

* Corresponding author at: Institut National de la Recherche Agronomique, UMR 1210 Biologie et Gestion des Adventices, INRA/AgroSup Dijon/Université de Bourgogne, 17 rue Sully, BP 86510, F-21065 Dijon cedex, France. Tel.: +33 3.80.69.33.29; fax: +33 3.80.69.32.62.
E-mail addresses: helmut.meiss@dijon.inra.fr, helmeiss@web.de (H. Meiss).

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Table 1
Studies investigating the impact of vegetation cover on seed predation.

Reference	Location	Habitat	Seeds	Main predators	Findings	Vegetation cover
Mittelbach and Gross (1984)	Michigan, USA	Old fields	Biennials	Ants, rodents	Seed removal higher in undisturbed vegetation than with disturbed soil.	+
Gill and Marks (1991)	New York, USA	Old fields	Trees	Mice	Predation higher under cover of herbs (85%) than without (6%).	+
Povey et al. (1993)	Oxford, UK	Field margin	Weeds	Small mammals	Higher predation in dense and uncut grass swards.	+
Hulme (1997)	Jaén, Spain	Shrubland	Trees	Rodents >birds >ants	Increased predation with increasing vegetation height, rodents avoided open areas while the reverse was true of ants.	+
Manson and Stiles (1998)	New Jersey, USA	Old fields	Trees	Mice	Ground cover explained most of the variation in seed predation.	+
Kollmann and Bassin (2001)	Klettgau, Switzerland	Field margin	Weeds	Rodents, slugs » insects, birds	Predation reduced by harrowing, not by cutting.	+,0
Davis and Liebman (2003)	Iowa, USA	Crops	Weeds	Crickets	Predation doubled in wheat underseeded with red clover compared to wheat alone (lower cover).	+
Gallandt et al. (2005)	Maine, USA	Crops	Weeds	Invertebrates	Harpalus rufipes density and predation higher in vegetated treatments and crops with higher LAI.	+
Heggenstaller et al. (2006)	Iowa, USA	Crops	Weeds	Crickets, beetles	Positive correlations between predation and canopy light interception for different crops.	+
Booman et al. (2009)	Pampas, Argentinia	Crop stubbles	Weeds	Small mammals	Predation increased with canopy height of wheat stubbles adjacent to annual crops, but decreased in stubbles adjacent to grasslands.	+,–
Navntoft et al. (2009)	Canterbury, New Zealand	Crops	Weeds	Mainly birds	Positive impact of plant cover until maximum at 54–75% cover, then sometimes decreasing.	+,∩

+, positive impact of vegetation cover on seed predation rates; –, negative impact; 0, no impact; ∩, highest predation rates at intermediate vegetation cover.

were present at the same time (treatments one to four). Bare soil plots (treatment five) were also included to increase the gradient of vegetation cover. We first studied the hypothetical impact of vegetation cover on weed seed predation. We then tested whether predation rates differed between the factors crop species and cutting. Finally, we assessed whether the variation between the treatments could be predicted by vegetation cover. As the impacts may vary between weed species and predator guilds, we used dif-

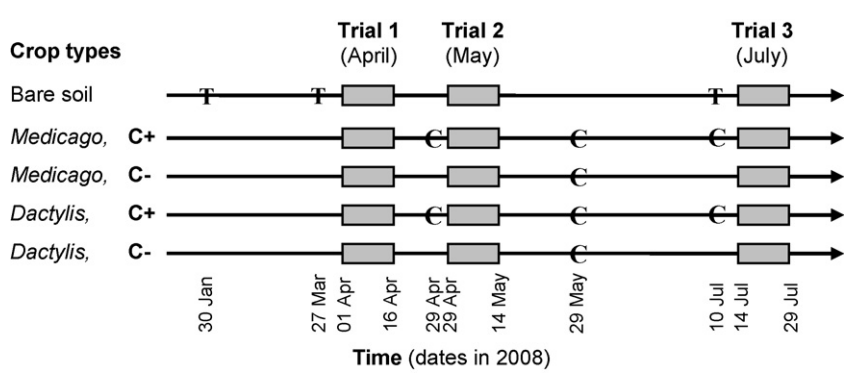

Fig. 1. Temporal overview of crop management in the five treatments. C, cutting dates; T, soil tillage dates; grey boxes, predation trials; C+, high cutting frequency; C–, low cutting frequency.

ferent weed species that are known to vary in their attractiveness to seed predators (Alignier et al., 2008) and selective exclusion treatments to separate seed losses caused by invertebrates and vertebrates.

2. Material and methods

The study was located at the INRA experimental farm "Epoisses" near Dijon in eastern France (47°20′N, 05°02′E, 230 m a.s.l.). Seed predation trials were conducted on plots of an ongoing cropping system experiment established in 2006. Five treatments were compared including two perennial forage crop species: *Medicago sativa* L. (alfalfa) and *Dactylis glomerata* L. (cocksfoot) that both received two contrasting cuttings (forage mowing, see below), and bare soil plots (no crop sown in 2008 but 5 cm superficial soil tillage to remove weed plants prior to the first and third trial periods, see Fig. 1). These five treatments were chosen (i) to create a gradient of vegetation cover and (ii) to test the impacts of, and interactions between, the factors crop species (legume *vs.* grass) and cutting (cut *vs.* uncut). Each treatment was replicated four times in a randomized complete block design. Plot size was 75 m^2 (7.5 m × 10 m) for all perennial crops and 35 m^2 (3.5 m × 10 m) for bare soil plots. All plots were arranged in an experimental field of about 0.75 ha which should reduce spatial heterogeneities in soil characteristics, crop succession histories and predator abundances, as the plot size was smaller than the foraging range of many seed predators (Menalled et al., 2006). Trials lasted for two weeks and were repeated three times (trials 1–3, Fig. 1).

2.1. Vegetation cover

Vegetation cover was estimated halfway through each trial period by measuring the photosynthetically active radiation on sunny days twice above (PAR_a) and three times below the canopy close to the soil surface (PAR_b) around the locations of the seed cards, using a Sunscan Canopy Analysis System SS1-UM-1.05 (Delta-T Devices Limited) with 64 light sensors on a 1-m stick. All measurements taken in the same plot at one period were averaged and a 'light transmittance rate' was calculated using the formula: PAR_b/PAR_a (Heggenstaller et al., 2006). The complement of light transmittance to 1, 'light interception rate', was used as an indicator of vegetation cover.

2.2. Weed seed predation

Weed seed predation rates were measured using "seed cards" (Westerman et al., 2003b). Three common annual weed species, *Alopecurus myosuroides* Huds., *Sinapis arvensis* L. and *Viola arvensis* Murray were tested at each trial, giving a total of 540 seed cards (three weed species × three exclusion treatments × five treatments × four replicate blocks × three trials). Twenty-five seeds per species were lightly glued to textile sandpaper cards (5 cm × 10 cm, grain size 100) using a spray adhesive (Sader, Bostik SA, Paris, France). This technique prevented seed losses caused by wind or rain, while most seed predators should still be able to remove the seeds (Westerman et al., 2003b). Nails (10 cm) were used to fix the cards horizontally on the soil surface. After exposure periods of 14 days, seed cards were removed and remaining seeds were immediately counted in the field.

Two different methods were used in each treatment to estimate the amount of accidental seed losses. (A) One third of seed cards was put into total exclusion cages (24 cm × 12 cm × 3 cm boxes made from metal wire gauze with 1 mm × 1 mm mesh size) which were permeable to wind and rain but would exclude any type of seed predator. (B) Plastic beads were presented instead of weed seeds. Results obtained with both control methods indicated that accidental seed losses were always marginal (A: 0–2% in 1-mm cages, B: 0–4% for plastic beads). It was thus not necessary to correct the measured seed predation rates for accidental losses.

To separate seed losses caused by different predator guilds, one third of seed cards were put into vertebrate exclusion cages (24 cm × 14 cm × 4 cm boxes made from metal fence wire with 12 mm × 12 mm mesh size), excluding all predators >12 mm, thus (at least) all birds and mammals. The seed loss rates on open (uncaged) seed cards were designated '*Total* seed predation', seed loss rates in the 12-mm cages '*Invertebrate* seed predation'; '*Vertebrate* seed predation' was calculated by subtracting '*Invertebrate* seed predation' from '*Total* seed predation'.

2.3. Statistical analysis

The response variable 'seed predation rate' was arcsin (square-root(y))-transformed to satisfy assumptions of normality and homogeneity of error variances. The explanatory variable 'light transmittance' was $\log_{10}(x+1)$-transformed, which increased the linearity of the models. Figures show untransformed data.

2.3.1. Overall variability

A three-way ANOVA model was fitted to analyze the impacts of 'trial period' (three levels), 'predator guild' (two levels), and 'weed species' (three levels).

2.3.2. Vegetation cover

The impact of vegetation cover was first analyzed by fitting ANCOVA models for *Total, Vertebrate*, and *Invertebrate* seed predation, containing the continuous variable 'light interception', and the two factors 'trial period' and 'weed species'. Owing to significant interactions, the impact of vegetation cover was also investigated for all weed species and trial periods separately using correlation analysis.

2.3.3. Treatment

To analyze the impact of 'treatment', ANOVA models were fitted that integrated the same variables as the ANCOVA models cited above, except that the continuous variable 'light interception' was replaced by the categorical variable 'treatment'. Owing to significant interactions, the impact of treatment was also analyzed for all trial periods and weed species separately using one-way ANOVA models.

2.3.4. Crop species vs. cutting

The relative importance of, and possible interaction between, the factors crop species and cutting were analyzed by fitting ANOVA models with three factors: 'crop species' (*Medicago–Dactylis*), 'cutting' (cut–uncut), and 'trial period' (May–July). The April data were excluded due to the lack of cut plots at this period.

2.3.5. Vegetation cover as a predictor

To analyze whether the differences between the treatments might also be explained by vegetation cover (two 'competing' variables), a 'variance partitioning' approach was used that can integrate continuous and categorical variables. It was simply based on several sequential ANOVA models with Type-I sums-of-squares (Type-I SOS) to calculate both the 'total' and 'exclusive' variances (Mac Nally, 2000) explained by each variable, using R (R Development Core Team, 2008). The common additive variance that may be explained both by 'treatments' and 'vegetation cover' ('joint' variance, Mac Nally, 2000) was obtained by subtracting the two exclusive variances from the total variance explained by both factors. Finally, the percentage of the variability among the treatments that may equally be explained by vegetation cover

Table 2
Overview showing (i) mean seed predation rates for three weed species; (ii) coefficients of determination of ANOVA models explaining 'seed predation rates' by 'treatment'(R^2); and (iii) coefficients of correlations between seed predation rates and canopy light interception (r). $N = 20$ for each weed species at each trial.

Predator guild	Trial 1 (April)			Trial 2 (May)			Trial 3 (July)		
Weed species	Mean predation (%)	ANOVA treatment (R^2)	Correlation light (r)	Mean predation (%)	ANOVA treatment (R^2)	Correlation light (r)	Mean predation (%)	ANOVA treatment (R^2)	Correlation light (r)
(A) Total									
A. myosuroides	21	ns	ns	15	ns	ns	51	$0.42^{\dagger}$	$+0.46^{*}$
S. arvensis	12	0.49^{*}	$+0.47^{*}$	2	ns	$+0.56^{**}$	47	0.48^{*}	$+0.59^{**}$
V. arvensis	58	0.85^{***}	$+0.46^{*}$	10	ns	$+0.44^{\dagger}$	58	0.46^{*}	$+0.52^{*}$
All species	30	0.21^{*}	ns	9	ns	$+0.31^{*}$	52	0.41^{***}	$+0.52^{***}$
(B) Vertebrates									
A. myosuroides	18	ns	ns	13	ns	ns	49	0.46^{*}	$+0.52^{*}$
S. arvensis	12	0.48^{*}	$+0.47^{*}$	2	$0.41^{\dagger}$	$+0.53^{*}$	42	0.39^{*}	$+0.48^{*}$
V. arvensis	50	0.78^{***}	$+0.52^{*}$	8	ns	$+0.51^{*}$	39	ns	ns
All species	27	0.25^{**}	+0.24	8	ns	$+0.34^{**}$	44	0.26^{**}	$+0.32^{*}$
(C) Invertebrates									
A. myosuroides	4	ns	ns	4	ns	ns	2	ns	ns
S. arvensis	1	ns	ns	1	ns	ns	4	0.54^{*}	$+0.37^{\dagger}$
V. arvensis	9	ns	-0.50^{*}	3	ns	ns	24	ns	$+0.51^{*}$
All species	5	ns	$-0.23^{\dagger}$	3	ns	ns	10	0.18^{*}	$+0.32^{*}$

ns, not significant.
† $p < 0.1$.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

was obtained by dividing the total amount of additive variance explained by 'light interception' by the total amount of additive variance explained by 'treatment'.

3. Results

Seed predation rates varied considerably between the three trials ($F_{2,338} = 34.5$, $p < 0.0001$, see Table 2 for mean values). Exclusion treatments (12 mm cages) suggested that vertebrates contributed much more to total seed losses than invertebrates ($F_{1,338} = 74.2$, $p < 0.0001$). Predation rates also differed between the three weed species ($F_{2,338} = 13.1$, $p < 0.0001$). Losses of *V. arvensis* seeds were highest during all periods and exclusion treatments except in May, where they were similar to *A. myosuroides*. Losses of *S. arvensis* were mostly lower than the two other species (Table 2).

3.1. Impact of vegetation cover

Weed seed predation was positively related to vegetation cover in most of the cases. In ANCOVA models, the additive effect of 'light interception' was highly significant for *Total* ($p < 0.0001$) and *Vertebrate* predation ($p = 0.0004$), but not for *Invertebrates*. Moreover, several two or three-fold interactions between light interception, weed species and trial period were significant but explained less variance than the main effects. When analyzing each trial separately, *Total* seed predation was always positively related to light interception (Table 2). Correlations were strongest in the July trial ($r = 0.52$, $p < 0.0001$), intermediate in May ($r = 0.31$, $p < 0.0149$), but not significant in April ($r = 0.19$, $p = 0.1491$). For *Vertebrates*, correlations were always positive but again weakest in April. For *Invertebrates*, correlations were only significant in July, probably because *Invertebrate* predation rates were very low in April and May (Table 2). When looking at each weed species-trial combination separately, predation rates increased with vegetation cover in 15 out of 27 individual cases, correlations were not significant in 11 cases, mainly for treatments with low overall predation levels, and only one negative correlation was detected for *Invertebrates* feeding on *V. arvensis* in April (Table 2).

In three-way ANOVAs, the additive effect of 'treatment' was significant for *Total* ($p < 0.0001$), *Vertebrate* ($p < 0.0001$), and *Invertebrate* predation ($p = 0.0175$). Significant interactions with 'trial period' showed that the differences between the treatments differed with time. When calculating separate one-way models for each trial (but pooling all weed species), the differences between the treatments were significant for *Total* and *Vertebrate* predation but not for *Invertebrates* in April; differences were *always* significant in July but *never* in May, where predation rates were low in every crop (Table 2). A similar pattern appeared when analyzing each weed species-trial combination separately, but differences were more often significant for *S. arvensis* and *V. arvensis* than for *A. myosuroides*. In summary, 9 out of 27 individual models were significant at $p < 0.05$ and two at $p < 0.1$ (Table 2). In April, *Total* predation was high in all *Medicago* plots (averaging at 49%) and low in both *Dactylis* and bare soil plots (15–20%, Fig. 2). In May, predation was always low except in uncut *Medicago*, where it was significantly higher (20%). In July, the predation levels were highest in uncut *Medicago* and uncut *Dactylis* (both about 75%), lowest in bare soil plots (about 18%) and intermediate in cut *Medicago* (36%) and cut *Dactylis* (58%, see Fig. 2 for details). Cutting always had a negative impact, especially in *Medicago*, where it reduced the *Total* predation rates by about 53% in July and 77% in May, compared to 21% and 27% in *Dactylis*, respectively.

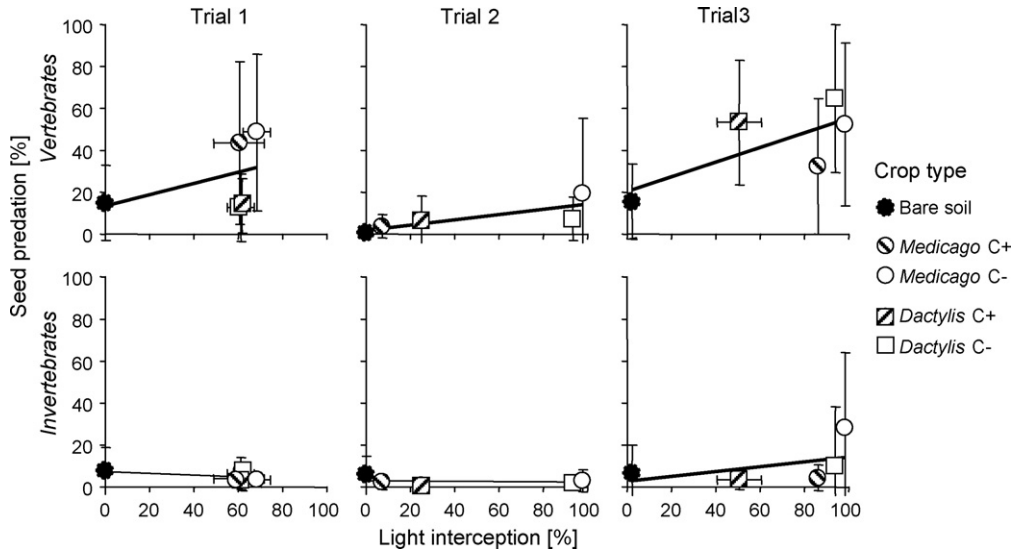

Fig. 2. Mean seed predation rates in five treatments as a function of vegetation cover (light interception). Each dot represents the mean value of three weed species and four replicates per treatment ($N = 12$), error bars show ±1SD. Bold lines indicate that the correlations between predation and light interception rates were significant (Table 2).

3.2. Crop species vs. cutting

For models of *Total* predation, the interaction between crop species and cutting was nearly significant ($p = 0.073$) while all other interactions were not significant. Interestingly, the additive effect of 'cutting' was highly significant ($p = 0.0004$) while 'crop species' had no additive effect ($p = 0.72$). A very similar pattern appeared for *Vertebrate* and *Invertebrate* predation, the only difference being that the additive effect of 'crop species' was significant for *Invertebrates* ($p = 0.047$). The impact of cutting was thus stronger for both predator guilds at both trial dates than the differences between the crop species.

The comparison of ANOVA and ANCOVA models described in Section 3.1 showed that ANOVA models including 'treatment' (five levels) explained more variance than the alternative ANCOVA models using 'light interception' (one regressor); the coefficients of determination (R^2) of the ANOVA models were 11–16 percent points higher than for the ANCOVA models. However, the adjusted R^2 differed only by 0–9 percent points, reflecting the lower number of parameters in the ANCOVA models.

The variance partitioning analysis indicated that 16–64% of the variance in predation rate explained by 'treatment' may equally be explained by 'light interception' (Table 3). This percentage tended to be higher for trials and exclusion treatments with higher predation rates (*cf.* Table 2). Fig. 2 supports the results of the statistical analysis and shows that differences in mean predation rates between the crop species and cuttings were mostly positively related to mean light interception rates, except for *Invertebrates* in April and May, where predation rates were low.

Variance partitioning also indicated that the sum of the variance explained by 'treatment' and 'light interception' (additive effects and interactions) varied between 18% and 55%, which was higher than the variance explained by weed species (1–41%, Table 3). Together, the two "environmental" variables determining the habitat quality of seed predators were thus more important than the differences between the weed species.

4. Discussion

Strong differences of seed predation rates between weed species have been frequently reported (e.g., Kollmann and Bassin, 2001; Westerman et al., 2003b; Mauchline et al., 2005). Interestingly, weed species preferences observed here were similar to findings of a previous study conducted in organic wheat fields in the same geographical area (Alignier et al., 2008). However, results suggested that predator habitat quality may be even more important than differences between seeds (Table 3).

Westerman et al. (2003a) observed high contributions of vertebrates to total weed seed losses like in the present analysis. In contrast, many other studies suggested that invertebrates cause

Table 3
Variance decomposition of seed predation rates. The additive variances of 'treatment' and 'light interception' are divided into exclusive and common parts. The variable 'weed species' has no common variance and no significant interactions with the two other variables.

Effect	Type of variance	Trial 1 (%)			Trial 2 (%)			Trial 3 (%)		
		Total	*Vertebrate*	*Invertebrate*	*Total*	*Vertebrate*	*Invertebrate*	*Total*	*Vertebrate*	*Invertebrate*
'Treatment'	Additive, exclusive	18	19	5	9	11	11	14	15	9
'Light' and 'treatment'	Additive, common	3	6	0	1	4	2	26	10	9
'Light'	Additive, exclusive	0	0	5	10	11	0	1	0	1
'Light * treatment'	Interaction	1	1	8	7	8	5	13	11	1
'Weed species'	Additive, total	41	30	41	16	11	5	1	1	17
Whole model		63	56	60	43	46	23	56	38	37
Total 'habitat effect'[a]		22	26	19	27	35	18	55	37	20
% of 'treatment' explained by 'light'[b]		16	24	(5)	(13)	(26)	(18)	64	39	49

[a] The total variance explained by additive effects of, and interactions between 'treatment' and 'light interception'.
[b] The percentage of variance explained by 'treatments' that may equally be explained by 'light interception'. Values are in brackets for the cases where the differences between the 'treatments' were already not significant (Table 2).

higher weed seed losses (e.g., Menalled et al., 2000; Gallandt et al., 2005; Holmes and Froud-Williams, 2005; Mauchline et al., 2005). Yet, some authors have reported methodological biases in the assessment of the relative impact of seed predator guilds. Some predators may avoid the exclusion cages even though their body size would permit them to pass through the mesh openings. Smaller invertebrates might also be unable to remove the seeds glued to the sandpaper cards (Shuler et al., 2008). However, possible underestimations of both the total predation rates and the contribution of invertebrates in this study would be systematic and would not challenge the comparisons between the treatments.

4.1. Vegetation cover

The impact of vegetation cover was nearly always positive among the trials, weed species, and exclusion treatments (Table 2). Positive impacts of vegetation cover were in line with most of the previous studies conducted in intensively managed and more natural ecosystems in various locations (Table 1). In our study, about 12% of the variation in seed predation rates could be explained by vegetation cover and this value was above 30% when global predation rates were high. Similar rates were observed by Heggenstaller et al. (2006). Vegetation cover was thus probably a major factor affecting weed seed predation rates.

Vegetation cover may change the habitat quality for seed predators by modifying (a) the microclimate (light, temperature) and soil characteristics (humidity, plant litter), (b) the presence of alternative food items such as leaves or insect larvae, (c) the presence of living or dead plant material that may be used as substrates for reproduction, and (d) the risk of being predated by carnivores (Manson and Stiles, 1998; Landis et al., 2005). Given this variety of possible mechanisms, it may be expected that different predator guilds react differently to the quantity (and quality) of vegetation cover. Several studies indicated that most granivorous beetles and rodents prefer denser vegetation (Hulme, 1997; Manson and Stiles, 1998; Honek and Jarosik, 2000; Shearin et al., 2008), while granivorous birds and ants may prefer open patches (Hulme, 1997; Moorcroft et al., 2002; Butler et al., 2005). While most of the previous studies focused either on vertebrates or on invertebrates (Table 1), our exclusion treatments indicated that vegetation cover increased weed seed predation by both guilds, except for periods with very low predation rates. Field observations and pitfall trapping suggested that both mice and granivorous beetles were abundant in the experimental field, while ants were rarely captured (data not shown). There is also no reason to assume that predation rates would be always linearly related to vegetation cover. To our knowledge, the study by Navntoft et al. (2009) is the first one to report non-linear impacts of vegetation cover on weed seed predation (Table 1). In our study, some relationships were rather exponential, e.g., for predation by *Invertebrates* in July (Fig. 2).

4.2. Crop species vs. cutting

Heggenstaller et al. (2006) found that seed predation rates follow the seasonal crop biomass development and would be temporarily reduced after mowing in perennial forage crops. Our results based on simultaneous comparisons of cut and uncut plots (reducing potential confounding temporal effects) support this hypothesis. In uncut crops, predation rates were higher in *Medicago* compared to Dactylis crops. Several authors reported tendencies towards higher seed predation in legume crops compared to non-legume crops (Andersson, 1998; Gallandt et al., 2005; Heggenstaller et al., 2006), but the reason why predators might prefer legume crops over grasses is still unclear.

In our experiment, the greater explanatory power of cutting compared to crop species indicated that vegetation quantity (biomass) was more important than vegetation quality, as already observed by Gallandt et al. (2005) for predation by invertebrates. The low predation rates observed on plots without any vegetation agree with this hypothesis. Differences between the five treatments were mainly linked to the differences in cutting and to the complete absence of plants in bare soil plots. This was probably the reason why quite large parts of the variation between the treatments could also be explained by canopy light interception (Table 3). The use of *continuous* environmental variables instead of *categorical* factors has proved to be more successful in predicting other biological phenomena including species richness and spatial distributions of organisms (Lindegarth and Gamfeldt, 2005). In our case, the use of a continuous measurable variable allowed (i) reducing the number of parameters in the models (parsimony/Occam's razor) and (ii) testing a more general hypothesis ("vegetation cover affects weed seed predation rates") which may be helpful to develop predictive models and facilitate the meta-analytical comparison of different studies (Lindegarth and Gamfeldt, 2005).

Results suggested that weed seed predation may be enhanced by maintaining a high and temporally extended vegetation cover. Farmers may thus potentially favour the ecological service of weed seed predation by implementing crop management practices that maximize vegetation cover on arable fields. This might be achieved by using cover crops, undersowing techniques, crop mixtures, or by including perennial crops in the rotations.

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D GENERAL DISCUSSION

Data from weed surveys on commercial fields and from the small-scale field experiments suggested that PFCs have strong impacts on the arable weed vegetation which is in line with the initial hypothesis. The large-scale weed surveys (Article 1) showed that current annual and perennial crops differed strongly in species composition (discussed in D.I.1). Comparisons between wheat fields following either perennial or annual crops as well as the analysis of several stages of a crop rotation before, during and after perennial crops using the space-for-time substitution design (Article 2) suggested that the inclusion of perennial crops in rotations based on annual grain crops also impacts the weed communities in the subsequent crop following PFC (seed details in D.I.2). While the large-scale studies were based on a high number of fields of a whole region during three years with a high variety of natural conditions and crop management techniques (information that was not available for analysis), different crop management treatment could be compared in the small-scale field experiment. This experiment suggested contrasting population dynamics and thus increasing differences in the communities between annual and perennial crops (discussed in D.I.3). A comparison of the behaviour of individual weed species in the large- and small-scale studies is provided in chapter D.I.4; reactions of functional groups, weed abundances and diversities are discussed in D.I.5 and D.I.6.

Results suggest that several mechanisms are involved in the effects of the impacts of PFCs on weeds (D.II). Mechanisms linked to (the absence of) soil tillage (D.II.1) and competition (D.II.2) are much better known than others linked to the regular hay cuttings (D.II.3), interactions between competition and disturbances (D.II.4) and weed seed predation (D.II.5), which were thus studied in more detail. Strengths and weaknesses concerning the different approaches are discussed after each section.

Given that the identified processes are intended to be integrated into mathematical models simulating the weed population dynamics as influenced by cropping systems and natural conditions, some suggestions for modelling formalisms are discussed in section D.III.

D.I EVIDENCE OF THE IMPACTS OF PFCS ON WEEDS

D.I.1 Differences in species composition between current crops

Comparisons of the weed community composition found in various crops showed that differences between annual and perennial crops were even higher than the well-known differences between autumn and spring-sown annual crops (Fig. 1 and Table 3 of Article 1). Indicator Species Analysis showed that most of the frequent weed species either preferred perennial lucernes (including *Taraxacum officinale*, *Veronica persica*, *Crepis sp.*, *Poa trivialis*, *Silene latifolia*, *Capsella bursa-pastoris*, *Picris sp.*) or annual crops (including *Mercurialis annua*, *Galium aparine*, *Fallopia convolvulus*, *Chenopodium album*, and *Cirsium arvense*) (Table 4 of Article 1). The results thus indicate that perennial lucernes suppressed many weeds that are widespread (and sometimes problematic) in annual crops while favouring other species. *Stellaria media* and *Alopecurus myosuroides* were the only frequent weed species (present in more than 5% of the fields) that showed about equal frequencies in annual and perennial crops (Fig. 2 of Article 1). Such large-scale comparisons of weed communities between annual and perennial crops have probably not been published previously, in contrast to the comparisons between different *annual* crops (e.g., Andreasen *et al.*, 1996; Murphy *et al.*, 2006; Fried *et al.*, 2008).

The main **advantages** of this large-scale study are linked to the random distribution of the fields and the use of data covering three years, which increased the spatial and temporal generality compared to the previously published studies, mainly based on small-scale field experiments (cf. literature review A.IV.1). However, this first approach has also three **limits**:

1) The large-scale weed surveys are only based on one survey per year and may thus miss weed species growing during other seasons.

2) As in other previous studies, weed communities in spring- and autumn-sown annual crops were not evaluated at the same dates, which might increase the differences in species composition. In contrast, the differences between perennial crops and autumn-sown annual crops are not concerned by this limit, as they were surveyed at the same period.

3) Finally, this approach does not say anything about the reproductive success of the recorded species, which will be important for long-term effects.

The first two limits could be addressed by the small-scale field experiment, where the weed vegetation was monitored on a much finer temporal scale during the whole vegetation period (see discussion on weed population dynamics, page 155 below). First evidence for long-term effects could be obtained by comparing fields with annual or perennial preceding crops and by following the development of the weed species composition during crop rotation using the space-for-time substitution design (discussed in the following paragraph).

D.I.2 Weed community trajectories during crop rotations

As long-term studies analyzing one or several cycles of long rotations with annual and perennial crops are very costly and impossible to conduct during 'standard' 2-4 years research projects, an alternative space-for-time substitution design was used in this work. It simultaneously compared a large number of fields being in different phases of such long crop rotations (before, at the beginning, at the end and after perennial crops). First, this analysis confirmed results of Ominski *et al.* (1999) who compared the weed species composition after either annual or perennial crops in Canada. Second, it suggested that the weed community composition varies in a cyclic way during the crop rotation. It thus allowed to retrace typical weed community trajectories during crop rotations including perennial crops and thus to better comprehend the differences in the weed species and functional groups composition in the following annual crop (see Article 2 for details).

Many species causing problematic infestation in wheat in cereal-based cropping systems were both less frequent and less abundant in wheat immediately following alfalfa as compared to wheat following a sequence of annual crops (main examples : *Galium aparine*, *Cirsium arvense*, *Sinapis arvensis*). On the other hand, perennial alfalfa favoured some species in the following wheat (main examples: *Taraxacum officinale*, *Silene latifolia*, *Veronica persica*), but most of those species would be likely to disappear quickly after some consecutive years of annual crops, because they were not frequent or abundant in wheat following annual crops, and are not considered as very harmful species in cereal-based cropping systems. As a consequence, the introduction of perennial alfalfa in annual crop sequences can be considered as a powerful mean to manage weeds, in spite of the low use of herbicide during the years of alfalfa.

Both in the large-scale comparisons and the field experiment, highest modifications in species composition away from the 'typical' weed composition in annual crops were observed during

the first year of the temporary grasslands. In contrast, species composition varied much less among 2-6 year old grasslands, which is consistent with observations by Critchley *et al.* (2006) in sown field margin strips in England.

While the large-scale study demonstrates the effect of perennial crops on weed communities in the following annual crop, future studies must also determine how long this effect may last. Canadian farmers estimated that weed control benefits of PFCs lasted for one, two, and three or more years (11%, 50%, and 33% of respondents, respectively, Entz *et al.*, 1995). While the large-scale studies allowed a good estimation of (instantaneous) species composition and species richness, abundance estimates were only based on one evaluation of the species frequencies on the 32 quadrats per field and per year, which is not very exact and strongly dependent on recent weed control actions. Therefore, high numbers of fields were required to detect the effects despite this variability. Future studies may thus also take into account the variability in crop management practices. Some of these shortcomings could be addressed by the field experiment discussed below.

D.I.3 Weed population dynamics under various crop management practices in the small-scale field experiment

Regular monitoring of the weed vegetation during the 2.5-years field experiment in Dijon-Epoisses also showed contrasted weed population dynamics in annual and perennial crops (chapter C.II, Manuscript 3). Differences in weed plant densities, diversities, biomasses and species composition were strongest between the annual and perennial crops, before all other contrasts concerning the crop management practices (see C.II.4.1 and summary in Table **11**). Many typical arable weed species showed decreasing plant densities in perennial crops and increases in annual crops (Fig. 13 and Fig. 14). Therefore, impacts of PFCs on weed communities observed in the field experiment are quite close to the large-scale weed surveys, despite the differences between the two studies (see the next section D.I.4 for details). Results of the field experiment are broadly also in line with several of the previous experiments in other cropping systems reporting weed suppression by PFCs (e.g., Schoofs and Entz, 2000; Bellinder *et al.*, 2004; Teasdale *et al.*, 2004; Albrecht, 2005; Heggenstaller and Liebman, 2006, and other studies reviewed in Article 1).

Among the three perennial crop **management factors** tested in the small-scale field experiment, the sowing date (autumn *vs.* spring) had strongest impacts on weed species

composition that may be compared to the differences between spring and autumn sown annual crops. However, these differences decreased with time in the emerged vegetation. In contrast, differences between the two crop species (alfalfa *vs.* cocksfoot) and the two cutting frequencies (3 *vs.* 5 cuts per year) appeared only later during the experiment and concerned mostly weed density and diversity, while species composition was rather similar (see details in the discussion of Manuscripts 3 & 4, chapter C.II). Such comparisons of several perennial crop management factors are rarely reported in the literature.

While the field experiment provided much finer estimations of plant emergence, plant survival and biomass production than the large-scale studies, other phases of the life cycles such as seed production could not be directly quantified but only roughly estimated from the weed biomass and the plant stages. Measurements of the weed emergence potential in the field by superficial soil tillage at four dates during the experiment did not succeed, due to unfavourable conditions for germination (lack of rain) at the chosen dates. Therefore, there is no evaluation of the temporal development of superficial seed bank densities. The final weed seed banks were studied by analyzing soil cores of all experimental plots with the direct germination method (modified from (Wellstein *et al.*, 2007) and (Cardina *et al.*, 2002a). Unfortunately, results of this analysis were not available for this thesis but will soon be published.

Future experiments should also test other management factors and treatment levels to account for the existing diversity in agronomic practices. In particular, the use of crop species mixtures (*e.g.*, legume + grass) should be tested as they may provide even greater weed suppression due to complementarities in growth dynamics and resources use as discussed in chapter C.II.4.4. Moreover, the cutting dates should be adapted to crop growth dynamics and tested in future experiments, as they might be even more important than the cutting frequency with fixed common cutting dates (see C.II.4.4 for details).

D.I.4 Comparison of weed species reactions between the large-scale surveys and the small-scale field experiment

When comparing the relative plant frequencies of individual weed species in the large-scale weed surveys in the Chizé region and the small-scale field experiment in Epoisses, many species showed quite similar behaviour in both studies (Fig. 21). Seven species had relative preferences for PFCs in both studies, about 15 species showed relative preferences for annual

crops, some species including *Poa annua* showed an intermediate behaviour in both studies, and only few species showed inconsistent reactions between the studies (see Fig. 21 for details). This result is remarkable, as the two studies differed in several aspects. While the Chizé study compared perennial alfalfa crops with six different annual crops (with various sowing dates) inserted in various crop rotations with a big variability in crop management practices (herbicides, soil tillage, sowing and cutting dates…) and in natural conditions in the region, the Epoisses experiment compared only one succession of annual cereal crops with two PFC species, alfalfa and cocksfoot, with different management practices (but all *without* herbicides) and a rather homogeneous weed species pool (weed seed adding at the beginning).

For instance, the high frequencies of *Echinochloa crus-galli* (ECHCG) and *A. retroflexus* (AMARE) in perennial crops of the Epoisses experiment (Fig. 21) occurred only in the spring-sown and never in the autumn-sown perennial crops. Such weed species would probably find good emergence and growing conditions in summer-sown annual crops which were not included in the Epoisses experiment. *Alopecurus myosuroides* (AMOMY) was clearly associated with the annual cereal crops in the Epoisses experiment. In the Chizé surveys, this species appeared with equal frequencies in annual and perennial crops. Its frequency in annual crops was probably lowered due to the fact that the six annual crops of the large-scale study included also 3 spring/summer-sown crops, where this species rarely grows. However, the reason why *Veronica persica* (VERPE) was associated with alfalfa in Chizé and with annual crops in the Epoisses experiment is still unclear.

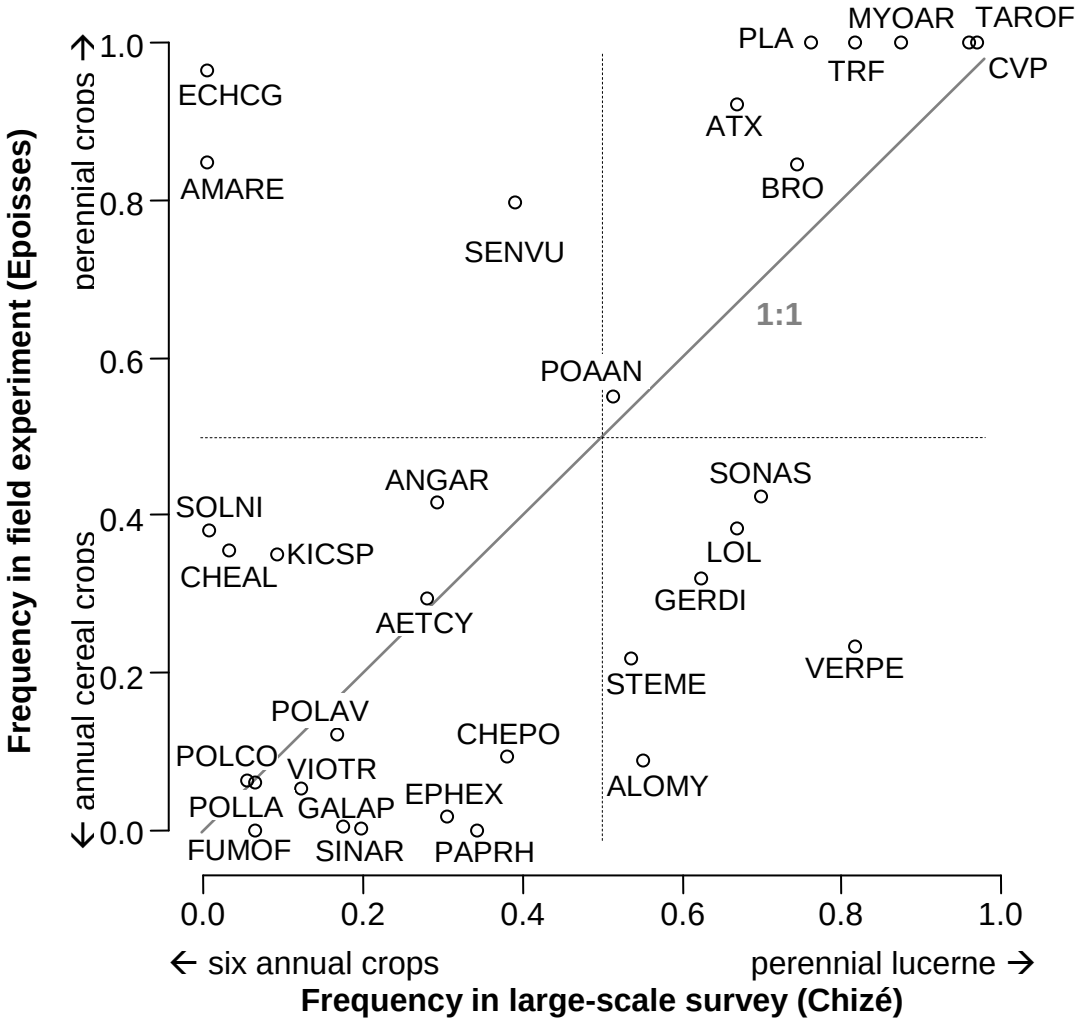

Fig. 21: Comparison of relative weed species frequencies in annual and perennial crops in the large-scale weed surveys (Chizé) and the field experiment (Epoisses).

See Annexe 3 for species codes. Rare species are not shown. **Chizé**: data from 2006, 2007 and 2008, perennial lucerne (*M. sativa*, 2 or more years old) and six annual crops apart those directly following perennial lucerne (see Fig. 2 of Article 1 for details). **Epoisses**: data from 2008 and 2009 only, perennial crops: *M. sativa* and *D. glomerata* (1.5-2.5 years old, all six crop treatments pooled), annual cereal crops: spring barley (following winter wheat, including only T9 and T11, excluding T10 with untilled stubble fields). The frequencies are calculated as follows: (species frequency in perennial crop) / (total species frequency in all crops). They are thus 0 if the species occurs only in annual crops and 1 if the species occurs only in perennial crops. Species near to the diagonal 1:1-line show similar behaviour in the two studies.

D.I.5 Functional groups

The different analyses based on the large-scale weed surveys on commercial fields, the field and greenhouse experiments suggest that the species suppressed and favoured by PFCs may be grouped into functional groups according to plant taxonomy, morphology and life cycle.

D.I.5.1 Annual *vs.* perennial weed species

Results from the different studies suggest that perennial forage crops favoured perennial over annual species (see Article 3 for some perennial weed species such as *Cirsium arvense* that did not follow this pattern). This has already been reported in previous studies (Ominski *et al.*, 1999; Albrecht, 2005; Hiltbrunner *et al.*, 2008) and agrees with ecological succession theory. Several mechanisms might be at the origin of this observation: (i) the absence of soil tillage may especially benefit species with longer life cycles, (ii) perennial species might be better adapted to temporally extended competition and (iii) to frequent hay cuttings than annuals (see details in the discussion on the mechanisms in chapter D.II below).

D.I.5.2 Small *vs.* tall or climbing species

Results from the different studies suggest that perennial forage crops suppressed in particular species with an upright and climbing broad-leaved species such as *M. annua*, *C. album*, *F. convolvulus* and *G. aparine*) compared to creeping species with a small height or with rosettes. This result corresponds to previous experimental studies, where forage crops suppressed broad-leaved weed species with similar upright or climbing morphologies such as *Abutilon theophrasti* Medik., *Amaranthus sp*., and sometimes even the same species such as *C. album* and *G. aparine* (Teasdale *et al.*, 2004; Albrecht, 2005; Heggenstaller and Liebman, 2006). Lian *et al.* (2006) observed that periodic cutting operations (each 2 month) suppressed the dominance of a climbing exotic weed in Chinese ecosystems, *Mikania micrantha* H.B.K and promoted the growth of native and other exotic species, mainly from the Alteraceae family, where rosettes are widespread.

D.I.5.3 Grasses vs. broadleaved species

While grasses showed higher survival rates and quicker regrowth after cutting compared to broadleaved species in the greenhouse experiments on individual plants, the whole group of grasses did not show increased frequencies and abundances neither in the large-scale weed surveys nor in the field experiment. This is in contrast to some previous studies in perennial

crops (Clay and Aguilar, 1998; Cardina *et al.*, 2002a; Teasdale *et al.*, 2004) and mown field margin strips (De Cauwer *et al.*, 2005). However, other previous studies reported reduced abundances of (annual) grass species including *Apera spica-venti* (L.)P.Beauv., *Avena fatua* L. and *Setaria sp.* (Norris and Ayres, 1991; Gill and Holmes, 1997; Schoofs and Entz, 2000; Cardina *et al.*, 2002a; Albrecht, 2005) while the perennial grasses *Elymus repens* (L.) Gould and *Poa sp.* sometimes profited from perennial crops (Andersson and Milberg, 1996; Clay and Aguilar, 1998; Teasdale *et al.*, 2004; Albrecht, 2005). Heterogeneous reactions of different grass species might be due to two opposed effects: most grasses probably have a good vegetative regrowth capacity (see chapter C.III), but hay cuttings may considerably reduce seed production of grassy weeds, especially all grass species that have tall and upright reproductive spires, which was also observed by Dalbies-Dulout and Dore (2001) for *A. myosuroides* in mown set-aside fields. Therefore, grasses may sometimes have high biomasses in perennial forage crops but this does not necessarily lead to high seed production and increasing populations (see chapter C.II). The success of seed production thus depends on the species' phenology and the exact cutting dates.

D.I.6 Weed abundance and diversity

While the community composition varied strongly between annual and perennial crops, and during the crop rotation of the space-for-time substitution design, variations in species diversity were smaller. At the field scale, higher species diversities were observed only for young perennial crops (Fig. 2 of Article 2), when species typical for annual and perennial crops co-existed temporally. This corresponds to the field experiments, where plant diversities were highest during the first month of the perennial crops (Fig. 12). Afterwards, weed diversities decreased at the field scale with the age of the perennial crops in both the large and the small-scale studies (which was mainly due to the reduction of typical arable weeds). Interestingly, these decreases were less strong than the decrease in weed abundances, improving the richness/abundance ratios compared to annual crops (Fig. 12). Moreover, the β-diversity (dissimilarity between the fields in the large-scale surveys) remained high (Fig. 2 of Article 2).

Sjursen (2001) observed a similar decrease in weed species numbers (and weed abundance) in the established vegetation during 3-year forage crops. In this study, Sjursen (2001) observed reduced weed abundances in the soil seed bank, but species diversities remained unchanged in the soil. In long-term experimental studies conducted by Sosnoskie *et al.* (2006), seed bank

diversities were even higher in crop rotations containing hay crops (alfalfa-ryegrass mixtures) compared to rotations containing only soybean or maize and monocultures of these annual crops.

As the nature of species associated with young and old alfalfa is very different from weed communities in wheats in annual crop sequences, the introduction of alfalfa also contributed to the overall diversity of the flora at the landscape level (in addition to the increased floristic richness in young alfalfa as compared to wheat crops).

Stable or increased plant diversities and improved richness/abundance ratios might be due to three mechanisms. 1) The reduced soil tillage (and reduced herbicide use on commercial fields) might lead to more stable habitats which would favour species diversity as predicted by the intermediate disturbance hypothesis (Connell, 1978). 2) Perennial crops might also show more small-scale habitat heterogeneities within the field than regularly tilled annual crops (Ominski *et al.*, 1999), which may favour plant species diversity, as shown *e.g.* by the review of Benton et al. (2003). 3) Finally, crop rotations including PFCs are more diverse than rotations including only annual crops, which may favour different species types in different crops and thus also increase the instantaneous plant diversity (cf. General Introduction).

D.I.7 Conclusion: PFCs, useful tools for Integrated Weed Management

The different large-scale analyses and the field experiment generally agreed with the main hypothesis of cyclic variation in weed abundance and species composition during the rotation cycle (Fig. 7 in the General Introduction). Perennial alfalfa suppressed several of the most widespread and most noxious weeds of annual arable crops. This may decrease weed pressure and thus the need for curative weed control in the following annual crops. At the same time, alfalfa favoured other plant species leading to stable or even slightly increased species diversities during the crop rotations. These new species are not known as mayor weeds in annual crops, and several of them (including *Rumex crispus, Crepis sp., Picris sp., Cerastium sp.*) showed already strongly decreased frequencies in the following annual crops (Table 3 of Article 2). It is thus not likely that the favoured species will cause strong weed problems in the following annual crops. The other way round, the results might also indicate that an ‘interruption of grassland periods with annual crops’ may be favourable for managing (perennial) grassland weeds such as *Rumex sp*. These results thus suggest that rotations of annual and perennial crops may contribute to weed control without reducing plant diversity.

Such diversified crop rotations could therefore be considered a valuable component of Integrated Weed Management.

D.II UNDERLYING MECHANISMS

The results suggested that the impacts of PFCs on arable weeds are governed by several mechanisms that affect different phases of the weed life cycle. Evidence comes from i) the analyses of weed species functional groups favoured and suppressed in and after PFCs in the large-scale weed surveys (chapter C.I), ii) the differences between weed community and population dynamics between annual and perennial crops and between the different crop managements of the field experiment (chapter C.II), and finally from the separate analyses of two potential mechanisms, namely iii) the post-cutting plant regrowth studied in the greenhouse experiments (chapter C.III) and iv) the weed seed predation tested in different field experiments (chapter C.IV).

The absence of soil tillage (A), the strong and temporally extended competition (B), and the frequent hay cuttings (C) were probably the most important factors governing the impacts of PFCs on arable weeds. In the following four paragraphs, I will briefly discuss how these factors (and interactions between them) probably affect the different phases of the life cycles of different weed species and species functional groups (see also the overview in Table 13 and the illustration in Fig. 20).

D.II.1 Absence of soil tillage (A)

The large-scale surveys and the small-scale field experiment both suggested that the absence of soil tillage in PFCs have two opposing impacts on weeds, to which different weed species may react differently. The absence of soil disturbance may i) reduce the germination and establishment of several typical annual weed species (through several mechanisms, Huarte and Arnold, 2003) while it may ii) increase the survival of established plants, which may be particularly favourable to longer living biennial and perennial species. These two mechanisms are probably a main cause of the reduced frequencies and abundances of typical annual weed species observed in the large-scale surveys and the field experiment and the increased frequencies of perennial (broadleaved) species in the large-scale surveys. Annual weed species (therophytes, Raunkiær, 1905) may survive the regular soil tillage typical for annual crops as seeds germinate preferentially after soil disturbance, while perennial species

(hemicryptophytes and geophytes, Raunkiær, 1905) may be particularly favoured by the absence of soil tillage due to e.g., their longer life cycles or vegetative reproduction.

D.II.2 Competition (B)

Temporally extended competition for growth resources in PFCs is partly an effect of the absence of soil tillage permitting the establishment of dense plant canopies and rooting systems of the perennial crop. Therefore, impacts of competition cannot be completely disentangled from the impacts of soil tillage discussed above. Both factors may favour plant species adapted to slightly later successional stages (later after the last disturbance of the vegetation), thus more 'K-selected' species with slower growth, later reproduction, higher life span, bigger final plant size, vegetative reproduction. In contrast, annual crops would rather favour species adapted to earlier successional stages (earlier after the last disturbance) thus more 'r-selected' species with a fast initial growth, short life cycle, reproduction by seeds, etc. The impacts of competition were particularly visible in the field experiment, where crop and weed biomass showed negative relationships especially during the first year. Treatments with bad initial crop establishment showed high initial weed biomass and the increase in crop biomass was accompanied by a decrease in weed biomass. While Clay and Aguilar (1998) observed reductions in crop-weed competition in older perennial forage crops, there was no sign that 2-6 years old alfalfa stands showed less weed suppression in the large-scale surveys (Article 2).

D.II.3 Hay cuttings (C)

Large-scale weed surveys, field experiments and the specific greenhouse experiments suggested that regular hay cuttings contributed to changes in the weed community composition. The consequences of cuttings might depend on (1) the level of damage due to cutting, and (2) the plant regrowth ability.

1) In the large-scale surveys (Article 2), the small-scale field experiment (Manuscript 3) and the greenhouse experiments (Article 4), species belonging to the functional groups of grasses and broadleaved species with rosettes or with a small and creeping morphology performed better than broadleaved species with a tall, upright or climbing morphology (including the most widespread and most noxious arable weeds such as *M. annua*, *C. album*, *F. convolvulus* and *G. aparine*). The most likely cause would be that larger parts of

the leaves (needed for photosynthesis) and buds (needed for regrowth) were destroyed for species belonging to the latter groups. Moreover, results of the greenhouse experiments showed that the residual green surface remaining after cutting is correlated to the plants' regrowth speed (Article 4) and that broadleaved weed species have a higher probability to survive if the terminal buds are *not* destroyed (unpublished results).

2) In the greenhouse experiments, post-cutting regrowth was also better for perennial species compared to annual species. Besides their longer life span, perennial species might also have more belowground reserves of carbohydrates that may be remobilized for regrowth after cutting. Differences between these species functional types observed in the large-scale studies (Article 2) are thus probably also caused by the impact of cuttings (and not only due to the absence of soil tillage).

Results of the greenhouse experiments in 2007 and 2008 also suggested that the regrowth of weed plants a) increased with plant biomass before cutting (for plants of the same age), b) decreased with plant age, c) increased with cutting height for broadleaved species, and d) decreased with the number of previous cuttings (see Articles 4 & 5 and two master thesis of Henriot (2007) and Bonnot (2008) co-supervised by the present author. The impacts of plant age and cutting height roughly corresponded to previous studies (El-Shatnawi *et al.*, 1999; Andreasen *et al.*, 2002), while the two other factors have rarely been investigated (Mager *et al.*, 2006; Wilson *et al.*, 2007). These observations on the interspecific variation of the regrowth ability may also be explained by the hypothesis postulating that the plant growth ability depends on the amount of carbohydrate resources remobilizable from roots and stubbles to replace the deficit caused by the absence of photosynthesis. An additional greenhouse experiment (presented in the co-supervised Master-I thesis (Bonnot, 2008) but not yet published in a journal), comparing the regrowth speed of cut plants with the initial growth speed of young uncut plants with the same (small) leaf area supported this hypothesis (Wilson *et al.*, 2007). The observed higher growth speed of cut plants was probably caused by remobilisation of belowground resources. Moreover, cut plants may also profit from the bigger rooting system compared to younger uncut plants. Such additional knowledge about the effects of cuttings as a function of the plants' regrowth ability may be useful for explaining and predicting the impacts of hay cuttings on arable weeds (see chapter D.III.2 for more details).

D.II.4 Interactions between cuttings and competition (B*C)

While the temporally extended competition will select for plant species adapted to later successional stages (K-selected species), the regular hay cuttings might have an antagonistic effect limiting the progression of successional stages (*e.g.* the establishment of woody species) in PFCs. There might thus be negative or positive interactions between the effects of cutting (C) and competition (B) (see details and references in the introduction of Article 6). Cuttings might, for example, reduce the aboveground competition for light (negative interaction) or the combination of competition and cutting may lead to disproportional reductions in weed regrowth (positive interaction). However, the measurements on small experimental plant communities in the greenhouse suggested that the negative effects of competition and cuttings were mainly additive (Article 6) and there were no signs that weed plants could profit from the temporally reduced competition after hay cuttings in the field experiment. The results rather suggested that the competitive advantage of the forage crops appeared in particular after the first crop cuttings (see chapter C.II).

D.II.5 Seed predation (D)

Weed seed predation is an ecological interaction between plants and animals that is not frequently investigated in agro-ecosystems, although recent studies suggested i) that weed seeds are an important food resource in arable fields (Manson and Stiles, 1998; Wilson *et al.*, 1999; Kollmann and Bassin, 2001) and ii) that seed predation may have strong impacts on weed population dynamics (Menalled *et al.*, 2000; Davis and Liebman, 2003; Westerman *et al.*, 2003c; Mauchline *et al.*, 2005). High predation rates observed in Articles 6-8 (about 30-80% of presented seeds were eaten during one or two weeks) support these two hypotheses. Weed seed predation may thus contribute to alleviate the ‘weed trade-off’.

A priori, weed seed predation may take place in any crop. However, it may be of particular importance in perennial crops and field margin strips for two reasons: 1) Soil tillage does not burry newly produced weed seeds into the soil, therefore, more seeds will stay exposed on the soil surface during the whole duration of the crop, thus for several years. (However, seeds may also be buried by animals). 2) The absence of soil tillage and the permanent vegetation cover may constitute a more stable habitat compared to annual crops that might favour the presence of different seed predators (Cromar *et al.*, 1999; Van Klinken, 2005). The field experiments in 2008 suggested that (i) weed seed predation rates in perennial forage crops are as high as in

field margin strips (compare Articles 7 and 8) and (ii) positively related to vegetation cover in perennial forage crops, explaining 3 % - 27 % of the variability (see Table 3 and references in Article 8). Due to these two reasons, the total seed predation cumulated over a whole year is probably more important in perennial crops compared to annual crops, which is in accordance with experimental results recently obtained in Iowa, USA (Westerman *et al.*, 2005; Heggenstaller *et al.*, 2006).

The results also suggested that weed seed predation rates differ strongly between weed species. Such differences between weed species were already detected in previous studies (White *et al.*, 2007). Interestingly, a comparison of the predation rates of seven common weed species between the studies in 2007 (Article 6) and 2008 (Articles 7 and 8) showed that the species preference order is quite stable across situations (see Fig. 22).

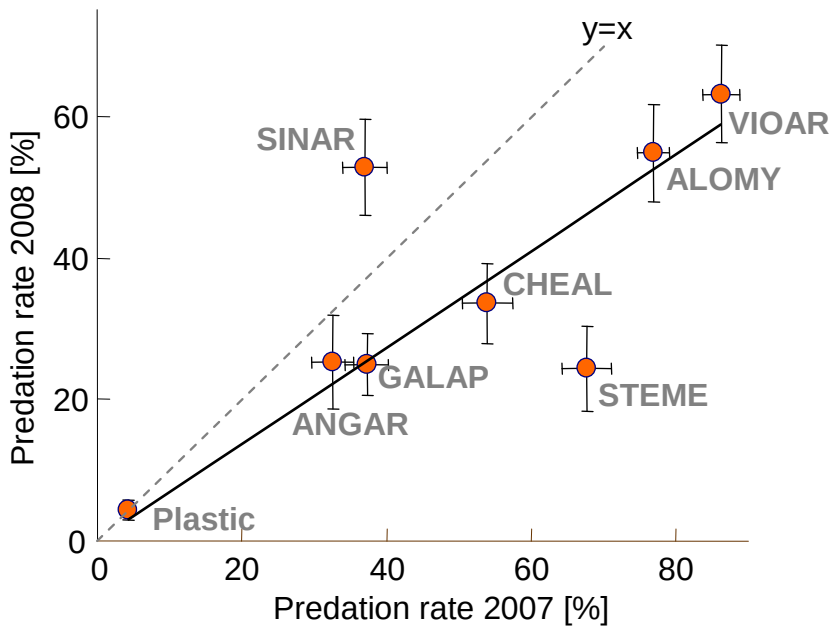

Fig. 22: Comparison of weed seed predation rates of the 2007 and 2008 experiments (cf. Article 6 and 8). Shown are mean ±SE predation rates for 7 weed species and plastic globules for control (see Table 7 or Annexe 3 for species codes). N=105 for the 2007 trial (Article 6), N=28 for the 2008 trial (Article 8, seven treatments confounded). The bold line shows the regression y=0.684x, R^2=0.535. Mean predation rates of all species except *Sinapis arvensis* tended thus to be higher in the 2007 experiment (means below the broken x=y line).

Although the reason for differences in predation rates among species is still unknown, such a preference order indicates that weed seed predation may contribute to changes in the weed community composition (White *et al.*, 2007). Moreover, weed seed predation would have lower impacts on perennial species and species that may reproduce vegetatively. Even if direct evidence is difficult to obtain, seed predation is probably an important factor underlying the impacts on weed population dynamics and weed community changes in and after PFCs. However, it is not yet clear which proportion of seeds is directly eaten by the predators and how many seeds are only removed and dispersed.

D.II.6 Overview of the underlying mechanisms

The results suggest that the impacts of PFCs on weeds are probably produced by several factors affecting different phases of the weed life cycle including seed germination and emergence, plant survival and vegetative growth, seed production and seed survival. The absence of soil tillage probably favoured perennial over annual weeds (at least for the broadleaved species), the temporarily extended competition probably reduced vegetative weed growth and seed production, mowings suppressed in particular the upright weeds while favouring several grasses and broadleaved species with rosettes and seed predation probably affected annuals more than perennial species. The importance of the different mechanisms probably varies with weed life stage: The impacts of cuttings increases with plant age (Article 4), the impact of competition is probably highest for young weed plants (Magda *et al.*, 2006), and soil tillage has both high impacts on seed germination but also on all other plant stages.

PFCs thus impose diverse selection pressures to wild plants. As the concept of IWM itself, the weed regulating function of PFCs is probably based on several mechanisms. Therefore, the risk of selecting ‘resistant’ weed biotypes among the suppressed arable weed species would be lower than for ‘single-mechanism’ weed control techniques. It is more likely that the imposed selection pressures modify the weed community assembly as observed in Articles 1-3 on the general impacts and Articles 4-8 on specific mechanisms.

Some of the mechanisms causing the impacts of PFCs on weeds could be clearly demonstrated in this project. However, the relative importance of them is difficult to determine and may strongly vary between local situations. Moreover, there may be other mechanisms and interactions that could not be investigated:

1) The absence of soil tillage and the high quantity of biomass in PFCs may also favour the establishment of a weed-suppressive mulch (Wiens *et al.*, 2006).

2) High vegetation cover (and mulch) also changes the light quality, temperature and humidity on the soil surface, which impacts weed germination (Huarte and Arnold, 2003).

3) Weed seed survival on the soil surface might not only be reduced due to seed predation, but also to seed decay.

4) Some perennial crops such as alfalfa (but also several annual crop species) might liberate allelopathic compounds inhibiting weed growth (Xuan and Tsuzuki, 2002).

5) Finally, improvements in soil structure and fertility, reductions in parasites or diseases of cash crops caused by PFCs might also ameliorate the growth and competitive ability against weeds of crops following PFCs.

D.III PERSPECTIVES: PREDICTING THE IMPACTS OF PFCS

D.III.1 Mechanistic models

Predicting weed population and community dynamics as a function of cropping system is a challenging issue due to the complexity of the system and the high number of interacting factors linked to crops, crop management practices, soil and climatic parameters and the diversity of weed species traits (Colbach and Debaeke, 1998). Mechanistic models simulating the various processes and cumulative effects involved in weed population dynamics are valuable tools for two main reasons. First, they have a heuristic value helping to better understand the complexity of the system, to identify possible interactions between processes and factors, and to rank the significance of the factors affecting the fate of the field/weed system. Second, they might be used for simulating a variety of cropping systems ('*in silico* experiments'), helping to identify solutions for weed management problems, and to perform *ex ante* evaluations of alternative cropping systems. *In silico* experiments might partly replace cropping system field experiments that are difficult to perform because of the long duration required for accounting for cumulative effects (Colbach and Debaeke, 1998). The mechanistic representation of involved processes is also a means to provide a large domain of validity for

the simulation model, although increasing the complexity of models increases the risk for over-parameterization, which may reduce the predictive robustness.

Such mechanistic models ('ALOMYSYS' and 'GENESYS') have been developed by the weed research group (BGA) in Dijon (France). The ALOMYSYS model simulates the population dynamics of *Alopecurus myosuroides* as affected by cropping systems, and GENESYS is dedicated to the population dynamics and gene flow at the landscape level between different wild and cultivated rapeseed (*Brassica napus*) and beet (*Beta vulgaris*) varieties (Colbach *et al.*, 2006a; Colbach *et al.*, 2006b; Colbach *et al.*, 2007; Sester *et al.*, 2008). FLORSYS is a new model currently under development[19] using basically the same principles, but simulating the dynamic of the whole plant community (several weed species and the crop), hence accounting for the differences in weed traits across the species, and for their contrasted response to cropping systems (Gardarin *et al.*, 2007a).

The models simulate the plant life cycle, representing the state of the system with a daily time step, and the various biological and physical processes affecting seed germination, seedling emergence, seedling growth and development, plant mortality and seed production (Colbach *et al.*, 2007). Most processes involved in weed population and community dynamics may already be simulated by the plurispecific FLORSYS model, including the impacts of soil tillage (types and dates) on seed distribution within the different soil layers, the effects of soil temperature and humidity on seed germination, the effects of herbicides on weed mortality, and competition with neighbouring crop and weed plants. However, the current versions of all three models account neither for losses of weed seeds due to predation nor for processes specific to perennial crops, e.g. the impacts of repeated hay cuttings on weed and crop growth. In the current versions, the life cycle of all weed plants is interrupted at soil tillage after crop harvest. Therefore, cropping systems including perennial crops cannot be simulated. The existing models must thus be extended with additional modules that simulate (i) the regrowth abilities of weed and crop plants after repeated cuttings and (ii) the impacts of seed predation. Knowledge obtained from this thesis might be used for supporting model construction of post-cutting weed and crop growth (see below). However, additional studies on weed seed predation are probably required before this complex ecological interaction between plants and animals can be formalized in a mechanistic way.

[19] http://www2.dijon.inra.fr/bga/umrbga/spip.php?article151 (accessed on 21 April 2010)

D.III.2 Predicting weed regrowth after cutting

According to the experimental results and discussions in Articles 4 and 5, the regrowth capacity of a given plant would depend on four main factors:

A) the green area remaining after cutting, determining the photosynthesis activity immediately after cutting,

B) the carbohydrate resources that can be remobilized from roots and stubbles for regrowth (to substitute the lack of resources and energy derived from photosynthesis due to the suppression of leaves),

C) the presence of intact buds/meristems where regrowth can start, and

D) the general growth conditions (see Table 1 and references in Article 4).

The probability of plant survival and the regrowth speed after cutting ('regrowth index' R) would thus be a (complex) function of these four factors. The simplest function might have the following form:

$$R = (A + B) * C * D$$

Three cases might lead to R = 0 (no regrowth, plant dies):

v) A+B = 0 (no leaf area remaining for photosynthesis *and* no carbohydrate resources available for remobilisation),

vi) C = 0 (no buds remaining for regrowth), or

vii) D = 0 (too bad general growth conditions).

In a simulation model, these four basic factors (A-D) would be determined by various underlying variables including i) the plant species (functional group), ii) the individual plant size (biomass), morphology (position of leafs and buds), and age (stage) at cutting date, iii) the cutting height, cutting dates and frequency, and iv) abiotic and biotic conditions determined by soil and climate variables, competition, parasitism, symbioses, crop and weed management. Most of these variables affect several of the four basic factors simultaneously (summarized in Table 1 of Article 4). Preliminary propositions how the four factors (A-D) might be simulated in a model are detailed in the following four paragraphs:

A, the 'green area remaining after cutting for photosynthesis', would be determined by the cutting height and by the weed plant height and morphology (vertical distribution of leaf area). Plant height and morphology will depend on i) the weed species (functional group) opposing tall and upright weed species *vs.* small and creeping species, ii) the plant age and stage at cutting date (very young plants are too small and therefore not touched by the cutting etc.) and iii) the plant growth resources and growth conditions (optimal water and nutriment availabilities may *e.g.* lead to bigger and taller weed plants, but high light availabilities may lead to smaller plants compared to plants grown in shadow, see references in Article 4). The FLORSYS-model already simulates the weed plant height and the vertical distribution of leaf area as a function of the phenology, biomass and light environment of each crop and weed plant on a daily timescale (Gardarin *et al.*, 2007a). However, the temporally extended competition in PFCs as well as the repeated cuttings and regrowth events may produce weed plants that may differ in morphology compared to weed plants grown in annual crops, which needs to be quantified by future studies and integrated in the current model.

B, the amount of 'carbohydrate resources that can be remobilized for regrowth', might be a function of i) the weed species (functional group), ii) the plant age, iii) the plant biomass before cutting, iv) the number of times and frequency the plant has previously been cut, and v) external conditions such as the temperature determining the rate of biochemical processes. Although previous experiments determined the absolute quantity of carbohydrates in plant roots and stubbles (Klimes and Klimesova, 2002; Rodriguez *et al.*, 2007), the 'quantity of carbohydrate that *can be remobilized for regrowth*' (B) cannot directly be measured. However, it may be implemented as a 'theoretical variable' in the model. According to the experimental results on several weed species, this variable would be:

- negatively related to the plant age (Fig. 6 of Bonnot, 2008 and Fig. 4 of Article 4),
- positively related to the plant biomass before cutting for plants of the same age (Table 4 of Henriot, 2007; Fig. 4 of Bonnot, 2008 and Fig. 3 of Article 4) [the belowground biomass is approximated by the aboveground biomass, which is possible as both are often closely related (Gedroc *et al.*, 1996; Wardle *et al.*, 2004)],
- negatively related to the number of previous cuttings (Fig. 2 of Article 4), and
- different between plant species functional groups (*e.g.* higher for perennials compared to annuals, Article 4).

Future studies must determine the shapes of these different relationships and the validity for a bigger number of species. For simplicity in the model, linear negative relationships with plant age may be assumed. However, the start of flowering or seed production might also cause somewhat abrupt decreases in the regrowth abilities for some species (illustrated in Fig. 23) which should be tested in future by comparing the regrowth capacity of a bigger variety of plant ages and stages.

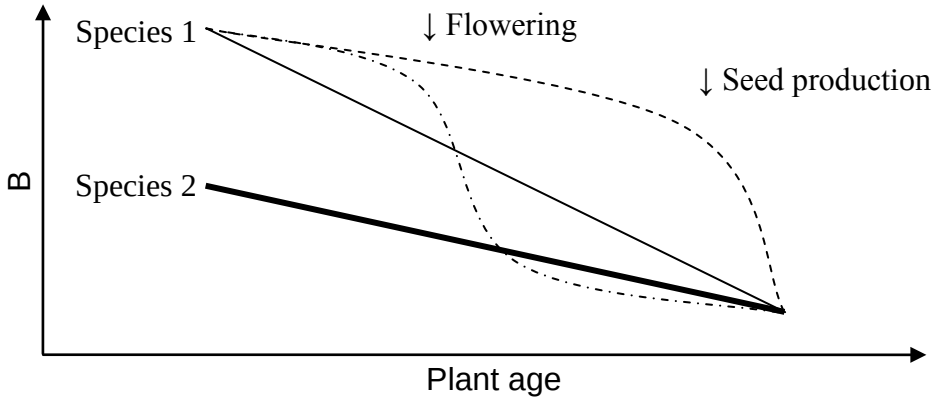

Fig. 23: Possible relations between the plant age and the plant's regrowth ability after cutting determined by the 'quantity of carbohydrate resources that can be remobilized for regrowth' (B) [g d°day^{-1}].

C, the 'presence of intact buds/meristems for regrowth', depends equally on the cutting height and the plant morphology (vertical distribution of *buds* in this case). As for 'A', the plant morphology would depend on the species (functional group), plant age at cutting date and the general growth conditions. While FLORSYS simulates the plant height and the vertical distribution of leaf area for each individual plant, the position of buds is currently not included in the model and rarely investigated by experimental studies. Concerning the interspecific variation, botanists and weed scientists might categorize most of the frequent weed species into 'functional groups' according to their morphology which may give first approximations for the vertical position of buds for different species. It is clear that the meristems of all grass species (from the Poaceae family) lie always near to (or below) the soil surface and are thus *a priori* not affected by hay cuttings. In contrast, buds of broadleaved species with an upright or climbing morphology may be partly or totally destroyed by cuttings (see *e.g.* the fate of *Chenopodium album* and *Amarantus retroflexus* after cutting in the greenhouse experiments) while broadleaved species with rosettes, a creeping morphology, a small size or many

branches ramifying near to the soil surface are likely to keep part of their buds. The intra-specific variation of plant height and morphology may be simulated in the same way as for 'A'.

D, the 'general growth conditions' determined by the availability of water, nutrients and light as affected by the soil, the climate and the crop management practices are already partly taken into account by the current versions of the FLORSYS and ALOMYSYS models. However, the general growth conditions may also *interact* with the impacts of cuttings and regrowth abilities of weed plants. Modifications in the growth resources and conditions (including weed control) may thus have stronger (or weaker) impacts on cut plants in PFCs compared to (uncut) weeds in annual crops. Some, but not all, of these interactions are already taken into account by simulating the impacts of the general growth conditions on 'A', 'B', and 'C' (detailed above). Experimental results reported in Article 5 suggest that the interactions between the impacts of cutting and competition are mainly additive (Fig. 3 of Article 5). The mechanistic representation of the processes should thus account for these additive effects of cutting and growth conditions. However, possible interactions with other factors are not yet accounted for by FLORSYS. Cut weed plants might *e.g.* be more vulnerable to fungal or bacterial pathogens than uncut plants which may also offer possibilities for combined mechanical and biological weed control (Kluth *et al.*, 2003).

At this stage, results from the greenhouse experiments might support some suggestions for basic formalisms to simulate weed and crop regrowth after cutting that could be introduced in the FLORSYS model. This could be based on the conceptual formula mentioned above: R = (A + B) * C * D.

Given i) a sufficient number of buds/meristems remaining after a cutting event (C > 0) and ii) favourable general growth conditions (D), the 'daily aboveground biomass increase' (ΔBM_j) of a cut plant depends on both the photosynthetic activity of the residual plant surface during day j ($\Delta BM_{phsynth\ j}$,) and on the remobilization of carbohydrates during day j ($\Delta BM_{remob\ j}$) :

$$\Delta BM_j = \Delta BM_{phsynth\ j} + \Delta BM_{remob\ j}\ .$$

Directly after the cutting event, the daily biomass production (ΔBM_j) would go down due to the loss of green surface (Fig. 24). During the following days, the lack of energy and carbohydrates may partly be compensated by remobilisation re-increasing ΔBM_j again

(illustrated in Fig. 24). Later, remobilisation will decrease again, which might be either due to a reduced demand (sufficient photosynthesis on newly established leaves) and/or due to a reduced offer (depletion of the belowground resources).

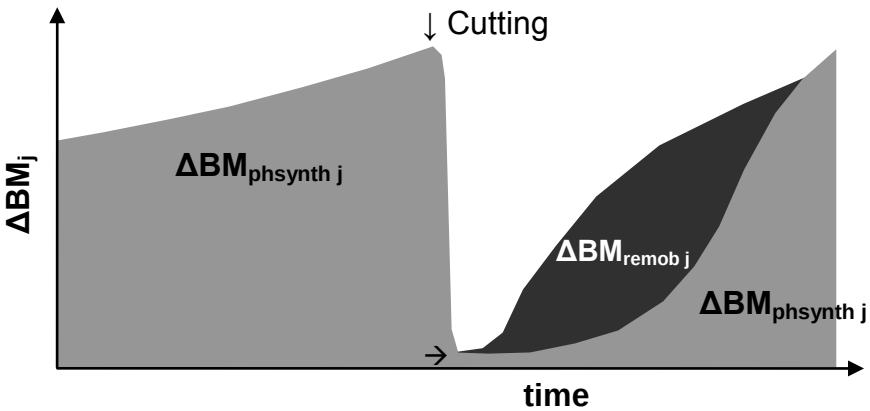

Fig. 24: Daily aboveground biomass increase (ΔBM_j) before and after a partial destruction of the photosynthetically active plant organs (cutting).
$\Delta BM_{phsynth\ j}$, daily aboveground biomass increase powered by photosynthesis; $\Delta BM_{remob\ j}$, daily aboveground biomass increase powered by remobilisation of belowground carbohydrate resources. The arrow (→) indicates the amount of biomass produced by photosynthesis on the residual green surface remaining after cutting.

$\Delta BM_{phsynth\ j}$ depends essentially on the plant's green surface and may be simulated by the FLORSYS model in the same way for uncut and cut plants (based on the energy balance of the plant estimated as a function of its light environment). In contrast, a new formula must be developed to estimate $\Delta BM_{remob\ j}$ that takes into account the considerations and experimental results discussed above:

$$\Delta BM_{remob\ j} = BM_{before} \cdot \alpha \cdot \max\left(0; T_{mean\ j} - T_b\right) \cdot \frac{LA_{th} - LA_{j-1}}{LA_{th}} \cdot \left(\beta \cdot BM_{before} - \sum_{1}^{j} \Delta BM_{remob\ j}\right)$$

The 'remobilization of carbohydrates during day j' ($\Delta BM_{remob\ j}$) would thus depend on:

- the aboveground biomass before cutting, $\mathbf{BM_{before}}$ (that is correlated to belowground biomass for a given species, Gedroc *et al.*, 1996; Wardle *et al.*, 2004);

- a remobilisation coefficient, α, determining the potential rate of remobilisation per day (α varies according to weed species, the number and frequency of times the plant has previously been cut and the plant age or phenological stage, such as illustrated in Fig. 24);

- the temperature interval between mean temperature at day j, $\mathbf{T_{mean\ j}}$ and the base temperature of plant growth specific of each species, $\mathbf{T_b}$; determining the speed of biochemical processes including remobilisation

- a coefficient reducing the remobilisation rate when the actual leaf area, $\mathbf{LA_{j-1}}$, converges during regrowth to a threshold leaf area, $\mathbf{LA_{th}}$ that determines the point where plant growth and respiration may entirely be powered by photosynthesis. (As this threshold is actually not known, it may be assumed for simplicity that it is equal to the known leaf area before cutting: $\mathbf{LA_{th}} = \mathbf{LA_{before}}$; in reality, $\mathbf{LA_{th}}$ might be lower, but the model will probably not be very sensitive to this parameter).

- The differences between the sum of biomass remobilized from cutting until day j, $\mathbf{\sum \Delta BM_{remob\ j}}$, and the total quantity of remobilizable carbohydrates, which is determined by the biomass before cutting, $\mathbf{BM_{before}}$, and $\boldsymbol{\beta}$, a coefficient determining the total part of biomass that may potentially be remobilized.

Therefore, remobilisation will decline and fade out when the available reserves are depleted or when enough new leaf area is established. The proposed formalism for simulating post-cutting regrowth is basically a model with 2 unknown parameters, α and β ($\mathbf{T_b}$ is already known in the FLORSYS model and $\mathbf{LA_{th}}$ might be assumed to equal $\mathbf{LA_{before}}$). Both parameters, $\boldsymbol{\alpha}$ and $\boldsymbol{\beta}$, would vary according to weed species, the number of times and the frequency the plant has previously been cut and the plant age or phenological stage, and might be estimated from the data obtained in the greenhouse experiments (chapter C.III). After implementing the model, an analysis of the model sensitivity to these parameters will have to be performed. It seems likely that the model will be highly sensitive to $\boldsymbol{\alpha}$ determining the remobilisation rate immediately after cutting.

D.III.3 Factors determining weed seed predation

Two factors were studied in detail that may affect the weed seed predation rate (differences between weed species and the impact of vegetation cover). Obviously, there may be numerous other factors that should be taken into account in a predictive model. To facilitate the development of future models, the large variety of factors might be organized according to a rather simple scheme based on 4 groups (illustrated in Fig. 25):

(i) factors determining *weed seed presence* and *abundance*, such as weed population densities, plant phenology determining the target period between seed shed and seed germination, spatial seed distribution and seed burial (Marino *et al.*, 2005; Heggenstaller *et al.*, 2006; Westerman *et al.*, 2008);

(ii) species-specific *seed traits* such as mass, size, seat coat and other physical and chemical characteristics determining seed attractiveness, palatability and nutritional value (White *et al.*, 2007) that would be at the origin of the consistent weed species preference order observed in the 2007 and 2008 seed predation experiments (cf. chapter C.IV and general discussion ;

(iii) factors determining *seed predator presence*, *abundance* and *activity* such as the regional predator species pool, predator dispersal abilities (Macdonald *et al.*, 2000b) and the local presence of favourable habitats for foraging and reproduction, as well as antagonists of the predators such as carnivores or parasitoids (Hulme, 1997; Van Klinken, 2005) (one of the most important factors determining habitat quality might be vegetation cover studied in Article 8);

(iv) the species-specific *diet, preferences and behaviour of the seed predators* which may vary according to the presence of alternative food items and the current energy need (hunger) of the predators.

‘Seed availability’ and ‘seed demand’ (Westerman *et al.*, 2003c) will thus be determined by (i) and by (iii)+(iv), respectively.

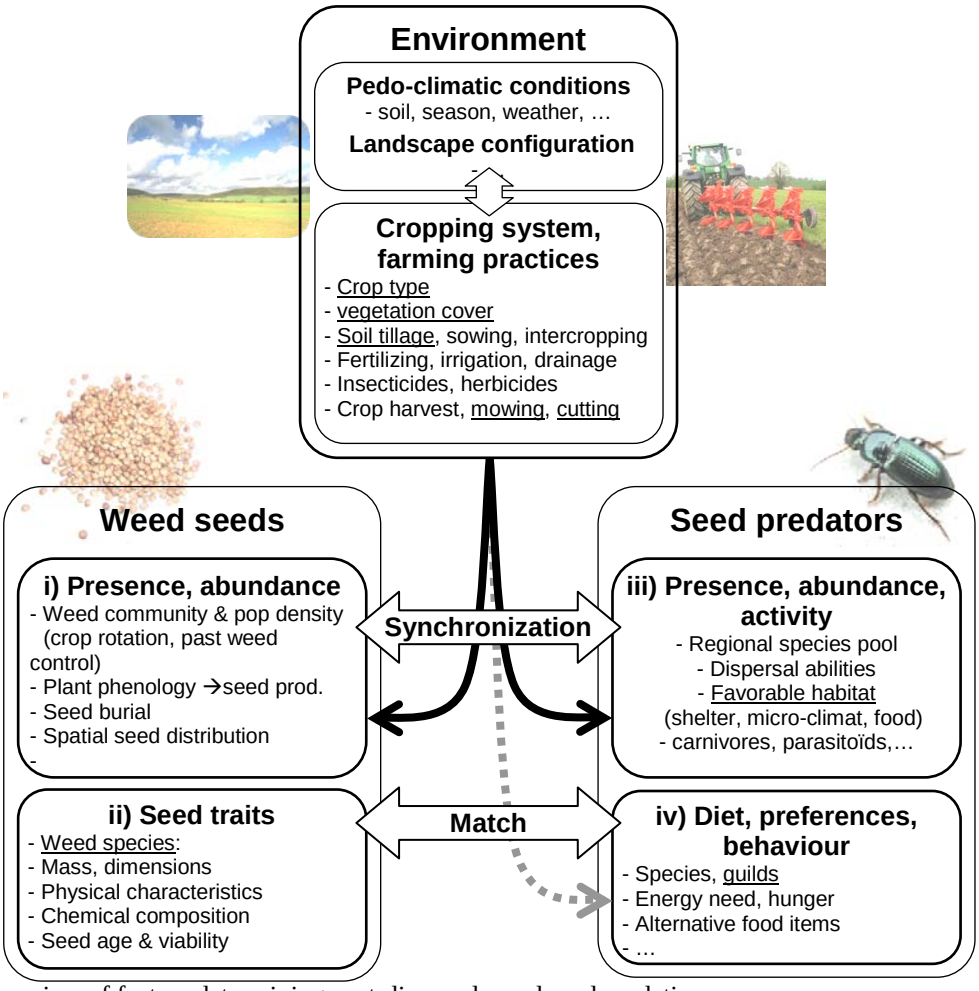

Fig. 25: Overview of factors determining post-dispersal weed seed predation.

Factors determining the presence and abundance of weed seeds (factor group i) as well as the presence, abundance and activity of seed predators (iii) vary according to the environment (upper box), which is determined by pedo-climatic conditions, landscape parameters and the cropping system (illustrated by the black arrows). These factors may thus be manipulated by the farmer through the choice of a crop and associated management practices (soil tillage, pesticides, harvest etc.). This is not the case for the specific traits of weed seeds (ii) and the diets, preferences and behaviour of the seed predators (iv). These characteristics might be considered as fixed parameters of the plant and animal species.

Following this scheme, seed predation may only take place if the predators' preferences correspond to the seed characteristics (iv) and if there is a temporal synchronisation between the presence of the predators and weed seed shed (iii, Fig. 25) (Van Klinken, 2005; Gallandt, 2006).

The species-specific characteristics of the seeds (ii) and of the predators (vi) are stable and can therefore not be manipulated to enhance weed seed predation. In contrast, most of the factors

governing the presence and abundance of seeds (i) and predators (iii) are strongly dependent on the environment such as the pedo-climatic conditions and landscape characteristics and, in the case of agro-ecosystems, on the cropping system and the different farming practices (Fig. 25). One of these environmental factors determining the habitat quality for seed predators, vegetation cover, has been shown in Article 8 to have a positive impact on seed predation rate. Future developments of models simulating weed seed predation might use this information. However, the lack of mechanistic knowledge on the impact of vegetation cover, the differences between weed seeds and all the other factors still hampers the proposition of a mechanistic modelling framework at this stage.

D.IV GENERAL CONCLUSION

The results of this research project provide direct evidence that perennial forage crops might play a significant role in arable crop rotations, both by contributing to the management of weeds and by maintaining or increasing the floristic diversity. The typical trajectories of weed communities identified from the preceding crop to the crop following alfalfa in the space-for-time substitution design in the large-scale surveys were consistent with the more precise, longitudinal observations of community and population dynamics in the field experiment. In both studies, strong changes in the weed species composition away from the most noxious species in annual crops were observed. Two examples of weed species that were clearly suppressed by PFCs were *Galium aparine* and *Cirsium arvense*, two very competitive species often requiring specific supplementary herbicide applications in current cereal-based cropping systems. Most important, the effects of PFCs on weed communities were still marked in the subsequent annual crop, hence indicating that the impacts not only concerned the currently emerged flora, but also the belowground seed bank. The observations thus validated one hypothesis of the project, *i.e.* the value of PFCs as a significant component of Integrated Weed Management. Introducing PFCs in arable crop rotations is thus a powerful means for weed management, probably allowing reductions in herbicides or excessive mechanical weed control. Moreover, diversified crop rotations including annual and perennial crops creates highly variable selection pressures for weeds, and this may also reduce the risk for selecting herbicide resistant weed biotypes.

According to the large-scale surveys, the species richness and the richness/abundance ratios were somewhat improved in alfalfa compared to annual grain crops, increasing floristic

diversity (α-diversity). Due to the strong differences in species composition between annual and perennial crops exceeding the difference among annual crops, plant diversity will also be increased at the crop rotation level (corresponding to a 'temporal β-diversity') and therefore probably also at the landscape level.

Another feature of this research project is that a significant effort was devoted to analytical studies aimed at gaining more knowledge about the processes involved in the impacts of PFCs. Two processes were scrutinized by specific experiments:

- The dynamic **post-cutting regrowth** process of weeds and crops was clearly a major process to analyse. The first cuttings often drastically changed ratios between crop and weed biomass in the field experiment. The greenhouse experiments conducted on individual plants and small experimental communities did indeed demonstrate huge differences in post-cutting regrowth abilities between weed and cultivated species, explaining the effects of cuttings on the changes in speceis composition. Interestingly, the experiments also provided insights about other factors affecting post-cutting regrowth, namely the phenological stage and the plant biomass at cutting, and also the cumulative number of previous defoliations.

- The second investigated mechanism was weed **seed predation**, a process currently gaining much attention in the agroecology research community. Weed seeds are an important trophic ressource for various farmland animals all year round, and seed predation might contribute significantly to weed control. The experiments confirmed that seed predation could be quantitatively important, but also highly variable across species, seasons, and environmental conditions. Correlations observed between the level of seed predation and vegetation cover provided an early interpretation of the observed variability, but the question of weed seed predation opens a huge research area that needs to be further investigated.

Integrating large-scale analyses with fine-scale experimentations was a goal of the research program from its inception. This was sometimes exhausting to manage, but it helped building an consistant scheme. The large-scale analysis based on a big dataset from the collaborative research project ECOGER allowed the study of the effects of PFCs on weed communities and statistically demonstrating their impacts despite a high diversity of situations in terms of

natural conditions, weed species pools and cropping systems. The pluri-annual field experiment with its finer spatial and temporal scales allowed studying the impacts of crop management practices and underlying mechanisms. Finally, gaining additional knowledge about some of the underlying mechanisms was the main target of specific experiments , either in the greenhouse or in the field.

The project was also interesting because it is at the interface between two disciplines, agronomy and ecology. In line with typical research projects in agronomy, the research design was conceived so as to provide information about the elementary processes involved, while accounting for some variation in crop management practices as far as possible. On the other hand, methods used for identifying community trajectories during crop rotations and the use of the species functional group concept were derived from ecology. The investigation of trophic relationships among different organisms is also hardly ever addressed in the agronomy community, while it is a typical research area of ecologists.

The rationale of the research project was arranged with two main ideas. The first idea was that there is a need to alleviate the triple 'weed trade-off', thus (i) the need for weed control and management to avoid significant yield losses in arable crops, (ii) the need for reducing reliance on herbicide to improve the quality of water resources (*i.e.* decrease the concentration of herbicide residues), and (iii) the role of weed biomass as a trophic resource for different components of the biodiversity in agricultural areas. The second idea was that a new concept of cropping system, separating agro-ecological functions in different phases of a diversified crop rotation could be a means for alleviating this trade-off. The different studies showed some evidence in line with the initial hypothesis of dynamic changes of the weed communities caused by the integration of PFCs into crop rotations.

Thanks to the efficiency of PFCs in repressing noxious weed species typically abundant in annual cereal crops, and because this effect remains in the cereal crops grown after PFCs, the concept of long crop rotations with a time distribution of agroecological functions seems to have significant potential for reconciling agricultural production, environmental protection and biodiversity conservation. In this concept (described in A.III.7 and illustrated in Fig. 5 of the general introduction), annual crops, perennial crops and additional specific periods favourable to biodiversity, such as overwinter stubble fields, are rotated on the field. On the landscape scale, fields managed according to this rotation scheme would thus form a dynamic mosaic of patches where the different functions (production of annual 'cash' crops with less

intratns, production of perennial forage or biomass crops, and the provision of favourable habitats and food resources for wildlife) will be continuously provided. The proposed 'temporal separation' strategy might also be combined with the 'spatial separation' and the 'complete integration' strategies (illustrated in Fig. 5 in the General Introduction). In this way, the different strategies may be complementary. This shows that beneficial intermediate solutions may exist between the two extreme alternatives, 'complete integration' or 'complete spatial separation', formulated by Green et al. (2005).

Besides the advantages for biodiversity, facilitating the access of wild animals to different food resources in PFCs (and overwinter stubble fields) may also have a regulating impact on weed populations ('biological weed control'). This would correspond to a positive feedback useful for alleviating the 'weeds trade-off'.

Of course the work done during this PhD program does not cover all the interesting questions in the area of the agro-ecological management of weeds and other components of biodiversity involving perennial forage crops. The investigations presented in this thesis directly motivate various further research:

- Finalising a model of crop–weed competition dedicated to PFCs, accounting for the specific process of post-cutting regrowth and potentially of seed predation. Such a model would make it possible to conduct *in silico* experiments, testing alternative scenarios for agro-ecological management of arable fields.

- Conducting socio-economic evaluations of the cropping system concept with various agro-ecological functions fulfilled at different phases of the crop rotation. In regions where farm animals are currently rare, perennial forage crops may be replaced by other perennial crops grown for energy or for biomass (see chapter A.V.4). Future studies should verify whether they may have similar benefits as PFCs.

- Conducting additional investigations in the area of agro-ecology dealing with the complexity of the consequences of crop rotation. For example, there is a clear need for defining what is actually a diversified crop rotation. Such a research program could aim at defining an indicator of crop rotation diversity, which would probably be a new useful tool for explaining weed communities and characterising the agro-ecological value of cropping systems in a given region.

This PhD research project documented the possible role that diversifying arable crop rotation with PFCs could play for reconciling agriculture, environment and biodiversity. The list of potential research areas touched upon is not exhaustive. But it is hoped that this thesis contributed to increasing our knowledge needed for enhancing agricultural sustainability.

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ANNEXES

ANNEXE 1: KEY WORDS IN ENGLISH, FRENCH & GERMAN

English key words	Mot clés français	Deutsche Stichwörter
Agri-environmental scheme	Mesure agri-environnemental	Agrar-Umwelt Maßnahme
Agroecology	**Agro-écologie**	**Agrarökologie**
Alfalfa, lucerne (***Medicago sativa***)	**Luzerne,** alfalfa	**Luzerne,** Alfalfa, Schneckenklee
Biodiversity	**Biodiversité,** diversité biologique	Biodiversität, biologische Vielfalt
Biomass	Biomasse	Biomasse
Clover, trefoil, sweet clover (***Trifolium, Melilotus***)	**Trèfle,** mélilot	**Klee** (Rot-, Stein-)
Cocksfoot, orchard grass (***Dactylis glomerata***)	**Dactyle aggloméré** /pelotonné	(Wiesen-) **Knaulgrass**, Gewöhnliches Knäuelgras
Community composition	**Composition de communauté**	Zusammensetzung der (Art-) Gemeinschaft
Competition	Compétition	Konkurrenz
Cover crop	Culture de couverture, interculture	Zwischenfrucht
Crop rotation	**Rotation de culture**	**Fruchtfolge** (-wechsel)
Ecosystem service	**Service d'écosystèmique**	**Ökosystemdienstleistung**
Fallow, set-aside	Friche, jachère, gel des terres	Brache, Flächenstilllegung
Food chain /-web	Chaîne /réseau trophique	Nahrungskette /-netz
Forage, fodder crop, - plant	**Culture,** plante **fourragère**	**Futterkultur** /-pflanze
Grass, graminoids	**Herbe** (graminée)	**Gras**
Integrated (Weed /Pest**) Management (IPM /IWM)**	**Gestion intégrée des adventices** /mauvaises herbes /bioaggresseurs	**Integrierter Pflanzenschutz**
Integrated farming	Agriculture /production intégrée	Integrierte Landwirtschaft /Produktion /Integrierter Anbau
Ley farming, mixed cropping	**Agriculture mixte**	**Feldgraswirtschaft**
Mowing, hay cutting	**Fauche**, broyage	**Mahd**, Heu-Schnitt
Organic farming /agriculture	Agriculture biologique	Ökologischer Landbau, Biologische Landwirtschaft
Perennial /pluriannual **forage crop (PFC)**	**Culture fourragère pérenne** /pluriannuelle	**Mehrjährige** /ausdauernde **Futterkultur**, **Ackerfutterbau**
Population dynamic	Dynamique de population	Populationsdynamik
Regrowth after cutting	**Croissance post-fauche**	**Nachwachsen nach Schnittmaßnahmen**
Seed predation, granivory	**Prédation de graines**	**Samenprädation**
Soil cover	Couverture du sol	Bodenbedeckung
Soil tillage	Travail du sol	Bodenbearbeitung
Stubble field	**Chaume**	**Stoppelfeld /-brache**
Sustainable agriculture	Agriculture durable	Nachhaltige Landwirtschaft
Temporary grassland (TG)	**Prairie temporaire /artificielle**	**Temporäres Grünland**
Weed, segetal-vegetation	**Mauvais herbe, plante adventice,** plante messicole	**Unkraut**, Ungras, **Ackerwildkraut**, Segetalvegetation
Weed control /management	**Contrôle /gestion des mauvaises herbes**	**Unkrautkontrolle /-bekämpfung /Beikrautregulierung**
Yield	Rendement	Ertrag

The most important key words are in **bold.**

ANNEXE 2: WHAT IS A WEED?

The term 'weed' may be used for plants with a variety of attributes including: 'growing in an undesirable location', 'useless, unwanted', 'competitive and aggressive', 'persistence and resistance to control', 'appearing without being sown or cultivated', and 'unsightly'. In this thesis, 'weed' designates any plant, that has not deliberately been sown or planted but grows spontaneously at a place and time where it is not wanted (by farmers). (The French '*mauvaise herbe*' and the German '*Unkraut*' and '*Ungras*' are directly reflecting the aspect of undesirability). Due to the definition of weeds as unwanted plants *at a given place and time*, it is not possible to classify any plant species *per se* as a weed. Several characteristics of weeds are briefly discussed in the following.

Harmfulness vs. utility:

Weed plants may be considered as *undesired* because of obvious negative effects on crops including competitive yield losses and harvest contamination (see Ch. A.II.1) or toxicity to man and animals. On the other hand, species commonly designated as weeds may also have positive effects on the agro-ecosystem: They may *e.g.* provide soil cover, which may reduce soil erosion and nutriment leaching at places and times where the crop is absent. They may also provide food resources and habitat for animals (see Ch. A.II.3). Several plant species frequently considered as 'weeds' may also be used as feed for animals or for producing human food or pharmaceutics (e.g. *Amaranthus retroflexus, Chenopodium album, Sonchus oleraceus, Spergula arvensis, Solanum nigrum*). Weeds might also be exploited for their genetic resources: by crossing crops with related weed species, plant breeders may introduce some desired traits of the weed species (e.g. resistances to pathogens, tolerances to climatic conditions). The same species may thus be considered 'harmful' and 'undesired' in some circumstances and 'useful' in others.

Cultivated vs. wild species:

In agro-systems, *all* plant species other than the actual crop(s) may be called weeds, thus including even 'volunteers' of other crop species or varieties sown in the past or on adjacent fields. Some weed species are very similar to crop species (weeds mimicking the crop), or even identical in the case of crop volunteers. Crop and weed species of the same families may sometimes cross and form fertile hybrids, that are well adapted to the crop management and difficult to control. This may be particularly problematic for crossings between weeds and

genetically modified crop varieties e.g. with herbicide resistances. The selective control of weed plants that are similar to the cultivated crop is most challenging, especially in the case of monocultures and simple crop successions.

Aesthetics:

'Weed' plants may be perceived as aesthetically *unattractive*, which may be one reason for classifying them as unwanted. On the other hand, several 'weed' species may also be *appreciated* due to a 'nice' or interesting appearance and colourful flowers increasing the attractiveness of agricultural landscapes. Moreover, other plants without special attractiveness are generally not considered as weeds if they are growing in more natural habitats. The *appeal* of a plant is thus also no good criterion to classify a species as a weed ('One man's flower is another man's weed').

Origin:

A big number of the arable weed species currently found in Europe have been introduced since longer or shorter times. This fact is reflected in one of the French words for weed, '*adventice*' that comes from the Latin '*adventicius*', meaning 'foreign'. Many weed species probably originate form the steppes in the Persian region (south of the Caspian Sea) (as do many cereal crops) and came to Europe since the development of agriculture about 7000 years ago. These species are called 'archaeophytes' and include species such as *Centaurea cyanus*. Archaeophytes may be distinguished from 'neophytes', which came to Europe after the 15th century. Some weed species may also have their origins in Europe ('native' species or 'apophytes'), living probably in rather small habitats with regular natural disturbances such as river banks.

Ecological requirements and habitats:

Most arable weeds are characterized by fast growth and high reproductive output (big number of small seeds or fast vegetative spread), that may quickly invade after disturbances. Therefore, they may be called 'ruderals' or 'r-selected' species. This aspect is stressed by the weed definition used by Baker (1974): '*a plant is a weed if, in any specified geographical area, its populations grow entirely or predominantly in situations markedly disturbed by man (without, of course, being deliberately cultivated plants)*'. Most weeds are well adapted to frequently disturbed habitats such as arable crops, gardens or construction sites, but some species may also be found in more natural habitats ("facultative weeds", Sutcliffe and Kay,

2000). The majority of arable weeds are annual species (therophytes, Raunkiær, 1905) that survive the unfavourable season and the yearly soil tillage in arable fields as seeds. However, weeds may also show strong differences in their ecological niches defined by the requirements for light and nutrients, the tolerance to competition and to physical and chemical disturbances. Several species are mainly found in certain crop types, soil types and climatic conditions (specialists) while others are rather generalists.

Distribution and status:

Today, a quite high number of weed species is found in various regions in temperate climates all around the world. Some species show increasing population dynamics and expanding geographical areas ('invasive species') while others are decreasing and locally or globally threatened to extinction and therefore included in Red Lists (Sutcliffe and Kay, 2000). Note that *both* categories may include 'native' and 'exotic' species (see 'Origin')!

ANNEXE 3: WEED SPECIES OF THE LARGE-SCALE SURVEYS

A total of 197 weed taxa were distinguished in the large-scale weed surveys in Chizé comprising 161 species and 36 groups of several species of the same genus, which were pooled together due to determination difficulties (see Table 14 for a complete species list). The overall frequency of occurrence of these taxa closely followed a negative exponential distribution with few frequent and many rare species (see Fig. 26 for details).

Table 14: Weed species of the large-scale surveys (Chizé).

Name contains species, groups of species (separated with '+'), sometimes with undefined species ('*sp*'), and genera without any determined species ('*spp*'). **Codes** are 5-letter Bayer/WSSA computer codes (3 letters for the genera, 2 for the species) or 3-letter genera codes. **Freq**uencies designate the absolute number of micro-plots in the Chizé weed surveys where the species has been observed out of 18441 micro-plots in total (confounding all seven crops and three survey years). **Life cycle** distinguishes three categories: annual species (A), perennial species (P) and intermediate species (I, with biennial or variable life cycles). Mono/Dicot distinguishes grasses (monocots, M) and broadleaved species (dicots, D). **Morphology** distinguishes four morphological types for the broad-leaved species. **FG**, Functional Group, distinguishes eight types of species based on the three criteria life cycle, number of cotyledons and morphology (see methods of Article 2 for details on FGs).

Name of species /genera	Code	Freq.	Life cycle	Mono/Dicot	Morphology	FG
Achillea millefolium	ACHMI	1	P	D	rosette	6
Adonis spp	ADO	56	A	D	upright	1
Aegopodium podagraria	AEOPO	5	P	D	rosette	6
Aethusa cynapium	AETCY	70	A	D	rosette	4
Agrostis stolonifera +sp	AGSST	26	P	M	grass	8
Alliaria petiolata	ALAPE	4	I	D	upright	5
Allium spp	ALL	69	P	M	upright	8
Alopecurus myosuroides	ALOMY	1686	A	M	grass	7
Amaranthus retroflexus	AMARE	401	A	D	upright	1
Ambrosia artemisiifolia	AMBEL	23	A	D	upright	1
Ammi majus	AMIMA	290	A	D	rosette	4
Anagallis arvensis	ANGAR	1637	A	D	creeping, other	3
Anagallis foemina	ANGCO	31	A	D	creeping, other	3
Anthemis	ANT	11	A	D	rosette	4
Anthriscus caucalis	ANRCA	13	A	D	rosette	4
Anthriscus sylvestris	ANRSY	15	P	D	rosette	6
Apera spica-venti	APESV	18	A	M	grass	7
Aphanes arvensis	APHAR	919	A	D	creeping, other	3
Arabidopsis thaliana	ARBTH	24	A	D	rosette	4
Arctium lappa	ARFLA	5	I	D	rosette	5
Arenaria serpyllifolia	ARISE	273	A	D	creeping, other	3
Arrhenatherum elatius	ARREB	53	P	M	grass	8
Artemisia vulgaris	ARTVU	18	P	D	upright	6
Arum sp	ABG	2	P	M	upright	8

Name of species /genera	Code	Freq.	Life cycle	Mono/Dicot	Morphology	FG
Aster squamatus	ASRSQ	3	A	D	rosette	4
Atriplex patula +prostrata +sp	ATX	1201	A	D	upright	1
Avena fatua	AVEFA	828	A	M	grass	7
Barbarea intermedia	BAR	4	I	D	rosette	5
Bellis perennis	BELPE	5	P	D	rosette	6
Bifora sp	BIFSS	6	A	D	rosette	4
Brassica nigra	BRSNI	119	A	D	upright	1
Bromus sterilis +mollis +sp	BRO	665	A	M	grass	7
Bryonia dioica	BYO	4	P	D	climbing	6
Buglossoides arvensis	LITAR	9	A	D	upright	1
Bupleurum subovatum	BUPLA	4	A	D	upright	1
Calepina irregularis	CPAIR	227	A	D	rosette	4
Calystegia sepium	CAGSE	299	P	D	climbing	6
Capsella bursa-pastoris	CAPBP	1836	A	D	rosette	4
Cardamine hirsuta	CARHI	76	A	D	rosette	4
Carduus spp	CRU	27	P	D	rosette	6
Carex spp	CRX	3	A	M	upright	7
Centaurea cyanus	CENCY	81	A	D	upright	1
Cerastium arvense +glomeratum	CER	355	A	D	creeping, other	3
Chaenorrhinum minus	CHNMI	38	A	D	upright	1
Chenopodium album	CHEAL	1956	A	D	upright	1
Chenopodium hybridum	CHEHY	114	A	D	upright	1
Chenopodium polyspermum	CHEPO	2	A	D	upright	1
Cirsium arvense	CIRAR	1169	P	D	rosette	6
Cirsium vulgare	CIRVU	16	P	D	rosette	6
Convolvulus arvensis	CONAR	3106	P	D	climbing	6
Conyza sumatrensis	ERIFL	6	A	D	upright	1
Coronopus sp	COPSS	5	A	D	rosette	4
Crepis sancta +vesicaria +sp	CVP	649	A	D	rosette	4
Cynodon dactylon	CYNDA	57	P	M	grass	8
Dactylis glomerata	DACGL	134	P	M	grass	8
Datura stramonium	DATST	13	A	D	upright	1
Daucus carota	DAUCA	572	I	D	rosette	5
Digitaria sanguinalis	DIGSA	38	A	M	grass	7
Dipsacus fullonum	DIWSI	1	I	D	upright	5
Draba muralis	DRAMU	12	I	D	rosette	5
Echinochloa crus-galli	ECHCG	288	A	M	grass	7
Elytrigia repens[20]	AGRRE	333	P	M	grass	8
Epilobium tetragonum	EPIAD	65	P	D	upright	6
Erodium cicutarium	EROCI	28	A	D	rosette	4
Eryngium campestre	ERXCA	1	P	D	upright	6
Euonymus europaeus	EUOEU	2	P	D	upright	6
Eupatorium cannabinum	EUPCA	7	P	D	upright	6
Euphorbia exigua	EPHEX	143	A	D	upright	1
Euphorbia helioscopia	EPHHE	1162	A	D	upright	1
Euphorbia peplus	EPHPE	33	A	D	upright	1
Falcaria vulgaris	FALVU	92	P	D	rosette	6
Fallopia convolvulus	POLCO	5562	A	D	climbing	2
Festuca rubra +sp	FES	82	P	M	grass	8
Foeniculum vulgare	FOEVU	3	I	D	upright	5
Fraxinus excelsior	FRAOF	11	P	D	upright	6
Fumaria officinalis +sp	FUMOF	533	A	D	upright	1
Galium aparine	GALAP	1981	A	D	climbing	2

[20] (syn. *Elymus repens*)

Name of species /genera	Code	Freq.	Life cycle	Mono/Dicot	Morphology	FG
Galium mollugo	GALMO	8	A	D	climbing	2
Galium verum	GALVE	1	A	D	climbing	2
Geranium columbinum	GERCO	41	A	D	rosette	4
Geranium dissectum	GERDI	1016	A	D	rosette	4
Geranium molle	GERMO	153	A	D	rosette	4
Geranium robertianum	GERRO	5	A	D	upright	1
Geranium rotundifolium	GERRT	358	A	D	rosette	4
Hedera helix	HEEHE	25	P	D	climbing	6
Heliotropium europaeum	HEOEU	4	A	D	upright	1
Holcus lanatus	HOLLA	9	P	M	grass	8
Hypericum perforatum	HYPPE	18	P	D	upright	6
Hypochaeris radicata	HRYRA	2	I	D	rosette	5
Juncus bufonius	IUNBU	3	P	M	upright	8
Kickxia spuria +sp	KICSP	802	A	D	creeping, other	3
Knautia arvensis	KNAAR	2	P	D	upright	6
Lactuca serriola	LACSE	339	A	D	rosette	4
Lamium amplexicaule	LAMAM	547	A	D	upright	1
Lamium hybridum	LAMIN	6	A	D	upright	1
Lamium purpureum	LAMPU	826	A	D	upright	1
Lapsana communis +sp	LAPCO	163	A	D	rosette	4
Legousia speculum veneris	LEGSV	78	A	D	upright	1
Leontodon sp	LEB	1	P	D	rosette	6
Lepidium campestre	LEPCA	1	I	D	rosette	5
Leucanthemum vulgare	CHYLE	4	P	D	upright	6
Linaria spp	LIN	9	A	D	upright	1
Linum usitatissimum	LIUUT	26	A	D	upright	1
Lolium multiflorum	LOL	872	A	M	grass	7
Lycopus europaeus	LYAEU	3	P	D	upright	6
Malva neglecta +sylvestris +sp	MAL	204	I	D	upright	5
Matricaria perforata	MATIN	7	A	D	rosette	4
Matricaria recutita	MATCH	189	A	D	rosette	4
Medicago arabica	MED	1	P	D	upright	6
Melilotus spp	MEU	1	P	D	creeping, other	6
Mentha spicata	MEN	27	P	D	upright	6
Mercurialis annua	MERAN	5774	A	D	upright	1
Misopates orontium	ATHOR	10	A	D	upright	1
Muscari sp	MUS	27	P	M	upright	8
Myosotis arvensis +sp	MYOAR	931	A	D	upright	1
Ononis spinosa	ONO	2	P	D	upright	6
Ornithogalum umbellatum	OTGUM	75	P	M	upright	8
Orobanche spp	ORA	1	A	D	upright	1
Oxalis sp	OXASS	18	I	D	creeping, other	5
Panicum miliaceum	PAN	155	A	M	grass	7
Papaver argemone	PAPRH	804	A	D	rosette	4
Pastinaca sativa	PAVSA	4	P	D	rosette	6
Petroselinum segetum	PARSE	531	I	D	rosette	5
Petasites hybridus	PEDHY	3	P	D	rosette	6
Picris echioides	PICEC	880	I	D	rosette	5
Picris hieracioides	PICHI	577	I	D	rosette	5
Plantago lanceolata	PLALA	89	P	D	rosette	6
Plantago major	PLAMA	98	P	D	rosette	6
Plantago media	PLAME	1	P	D	rosette	6
Poa annua	POAAN	490	A	M	grass	7
Poa pratensis	POAPR	11	P	M	grass	8
Poa trivialis	POATR	1091	P	M	grass	8
Polygonum amphibium	POLAT	2	P	D	upright	6
Polygonum aviculare	POLAV	3104	A	D	creeping, other	3

Name of species /genera	Code	Freq.	Life cycle	Mono/Dicot	Morphology	FG
Polygonum lapathifolium	POLLA	50	A	D	upright	1
Polygonum persicaria	POLPE	444	A	D	upright	1
Potentilla reptans	PTLRE	43	P	D	rosette	6
Primula sp	PRI	3	P	D	rosette	6
Pulicaria dysenterica	PULDY	4	P	D	upright	6
Ranunculus acris	RANAC	1	P	D	upright	6
Ranunculus arvensis	RANAR	4	A	D	creeping, other	3
Ranunculus ficaria	FICVE	3	P	D	creeping, other	6
Ranunculus parviflorus	RANPF	172	P	D	creeping, other	6
Ranunculus repens	RANRE	35	P	D	creeping, other	6
Ranunculus sardous	RANSA	64	A	D	creeping, other	3
Raphanus raphanistrum	RAPRA	5	A	D	upright	1
Rapistrum rigosum +sp	RASRU	96	A	D	upright	1
Reseda lutea +sp	RES	531	I	D	upright	5
Rosa sp	Rosa	1	P	D	climbing	6
Rubia peregrina	RBIPE	2	P	D	climbing	6
Rubus fruticosus	RUB	362	P	D	climbing	6
Rumex acetosella	RUMAA	3	P	D	upright	6
Rumex conglomeratus	RUMCO	33	P	D	upright	6
Rumex crispus	RUMCR	271	P	D	upright	6
Rumex obtusifolius	RUMOB	135	P	D	upright	6
Salvia sp	SAL	1	A	D	upright	1
Saxifraga tridactylites	SXFTR	1	A	D	rosette	4
Scandix pecten-veneris	SCAPV	105	A	D	rosette	4
Scleranthus annuus	SCRAN	5	A	D	upright	1
Scrophularia sp	SCUSS	2	A	D	upright	1
Senecio vulgaris +sp	SENVU	2188	A	D	upright	1
Setaria pumila	SET	597	A	M	grass	7
Sherardia arvensis	SHRAR	204	A	D	creeping, other	3
Sherardia sp	SHR	1	A	D	creeping, other	3
Silene latifolia	MELAL	1034	P	D	upright	6
Silybum marianum	SLYMA	177	A	D	upright	1
Sinapis alba	SINAL	5	A	D	upright	1
Sinapis arvensis	SINAR	1771	A	D	upright	1
Sisymbrium officinale	SSYOF	44	A	D	upright	1
Solanum nigrum +sp	SOLNI	1236	A	D	upright	1
Sonchus arvensis	SONAR	13	P	D	rosette	6
Sonchus asper	SONAS	2950	A	D	rosette	4
Sonchus oleraceus	SONOL	305	A	D	rosette	4
Spergula arvensis	SPRAR	10	A	D	creeping, other	3
Stachys annua	STA	116	A	D	upright	1
Stellaria aquatica	MYTAQ	1	A	D	creeping, other	3
Stellaria media	STEME	2054	A	D	creeping, other	3
Taraxacum officinale	TAROF	2061	P	D	rosette	6
Thlaspi arvense	THLAR	164	A	D	rosette	4
Thlaspi perfoliatum	THLPE	10	A	D	rosette	4
Tordylium maximum	TORMA	12	A	D	rosette	4
Torilis arvensis	TOI	387	A	D	rosette	4
Tragopogon pratensis	TROPR	10	P	D	upright	6
Tragopogon pratensis	TROPR	10	P	D	upright	6
Trifolium arvense	TRF	224	P	D	creeping, other	6
Tussilago farfara	TUSFA	2	P	D	upright	6
Urtica dioica	URTDI	24	P	D	upright	6
Valerianella locusta	VALLO	172	A	D	rosette	4
Verbascum thapsus	VESTH	6	I	D	rosette	5
Verbena officinalis +sp	VEBOF	228	I	D	upright	5
Veronica agrestis	VERAG	120	A	D	creeping, other	3

Name of species /genera	Code	Freq.	Life cycle	Mono/Dicot	Morphology	FG
Veronica arvensis +polita	VERAR	1194	A	D	creeping, other	3
Veronica hederifolia	VERHE	4856	A	D	creeping, other	3
Veronica persica	VERPE	4220	A	D	creeping, other	3
Vicia cracca +sp	VIC	54	P	D	upright	6
Viola arvensis +tricolor +sp	VIOTR	2630	A	D	upright	1
Vulpia myuros	VLPMY	3	A	M	grass	7

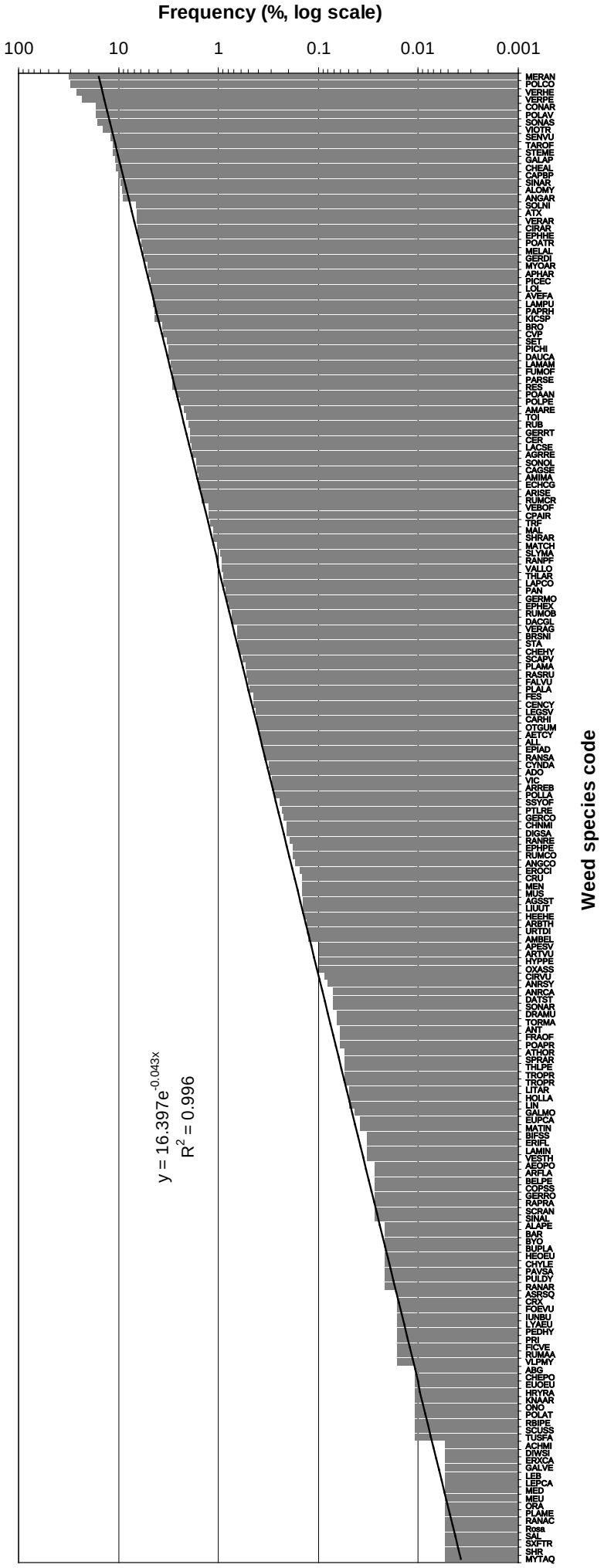

Fig. 26: Weed species frequency distribution in the large-scale weed surveys (Chizé).

See Table 14 for species codes and names. Frequencies were calculated as the number of micro-plots where the species was present on the total number of micro-plots surveyed (18441, pooling all 8 crops and 3 survey years) and plotted on a logarithmic scale.

134 out of the 197 taxa were present on less than 1% of the plots (less than 180 plots, rare species) while 13 species were present on more than 10% of the micro-plots (frequent species).

The most frequent species, *Mercurialis annua* (MERAN), was present on 5774 micro-plots (= 31.3 %), the 16 least frequent species on only one micro-plot (0.0054 %). The frequency distribution of the 197 taxa followed a negative exponential function (regression line, R^2=0.996). However, the four most frequent species had approximately two times higher frequencies than expected by the fitted exponential regression.

ERKLÄRUNG (DECLARATION FOR THE GIESSEN UNIVERSITY)

Ich erkläre: Ich habe die vorgelegte Dissertation selbständig und ohne unerlaubte fremde Hilfe und nur mit den Hilfen angefertigt, die ich in der Dissertation angeben habe. Alle Textstellen, die wörtlich oder sinngemäß aus veröffentlichten Schriften entnommen sind, und alle Angaben, die auf mündlichen Auskünften beruhen, sind als solche kenntlich gemacht. Bei den von mir durchgeführten und in der Dissertation erwähnten Untersuchungen habe ich die Grundsätze guter wissenschaftlicher Praxis, wie sie in der ‘Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis’ niedergelegt sind, eingehalten.

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Overview of treatments

CHAPTER C.I: LARGE-SCALE WEED SURVEYS

Table B1: Crop species surveyed in the first study (see **Table 2 in Article 1 ASD**).

Crop species	Type	Sowing season
Alfalfa (*Medicago sativa*)	perennial	autumn or spring
Winter wheat (*Triticum aestivum*)	annual	autumn
Oilseed rape (*Brassica napus*)	annual	autumn
Pea (*Pisum sativum*)	annual	autumn or spring
Sunflower (*Helianthus annuus*)	annual	spring-summer
Maize (*Zea mays*)	annual	spring-summer
Sorghum (*Sorghum bicolor*)	annual	spring-summer

Table B2: Groups of fields surveyed in the second study representing four stages of a crop rotation (see **Table 1 in Article 2 WRE**).

Group	Crop and precedent
a)	Wheat after annual crops
b)	Alfalfa 1 year
c)	Alfalfa 2-6 years
d)	Wheat after alfalfa

CHAPTER C.II: FIELD EXPERIMENT

Table B3: Nine crop treatments (T2-T11) of the Epoisses experiment (see **Table 6 of Manuscript 3** for details).

Treatment code	Symbol	Crop		Management		Intercrop	
		Type	Species	Sowing season	Cutting frequency	Autum soil tillage	Cover crop
T2 Med Aut C-		Perrennial	*Medicago sativa*	Autumn	3/y **C-**	/	/
T4 Med Aut C+		Perrennial	*Medicago sativa*	Autumn	5/y **C+**	/	/
T5 Med Spr C+		Perrennial	*Medicago sativa*	Spring	5/y **C+**	/	/
T6 Dac Spr C+		Perrennial	*Dactylis glomerata*	Spring	5/y **C+**	/	/
T7 Dac Aut C+		Perrennial	*Dactylis glomerata*	Autumn	5/y **C+**	/	/
T8 Dac Aut C-		Perrennial	*Dactylis glomerata*	Autumn	3/y **C-**	/	/
T9 WB T+		Annual	Wheat-Barley	See Table 4B		Yes **T+**	No
T10 WB T-		Annual	Wheat-Barley			No **T-**	No
T11 WB T+M		Annual	Wheat-Barley			Yes **T+**	**M**ustard

CHAPTER C.III: REGROWTH AFTER CUTTING

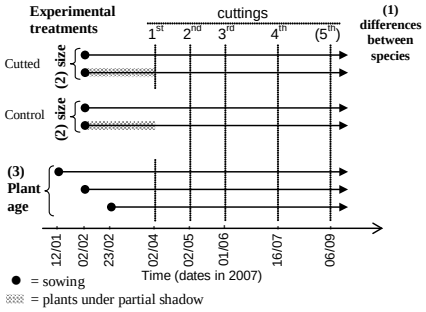

Fig. B1: Overview of the experimental treatments, sowing and cutting dates of the regrowth trials in 2007 (see Methods of **Article 4 JPDP** for details).

Table B4: Four treatments for interaction between competition (presence of alfalfa) and cutting (2x2 factorial design, see Methods of **Article 5 BMH** for details).

Treatment	Competition	Early cutting
A)	Weak (no alfalfa)	No
B)	Strong (alfalfa)	No
C)	Weak (no alfalfa)	Yes
D)	Strong (alfalfa)	Yes

CHAPTER C.IV: SEED PREDATION

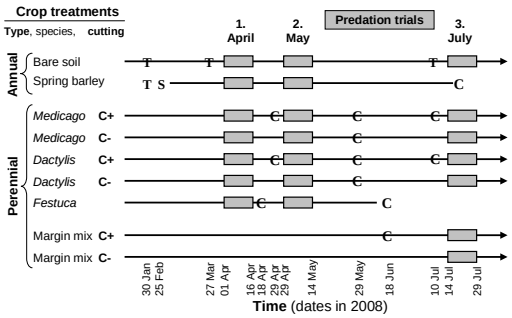

Fig. B2: Crop treatments of the seed predation study (cf. **Fig. 1 in Article 8 AGEE and Article 7**). T, soil tillage; S, sowing; C, cutting dates.