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**Dynamique spatio-temporelle des communautés adventices en réponse aux pratiques de gestion des sols et conséquences pour les processus de recyclage de la matière organique dans les vignobles une approche fonctionnelle**

Marie-Charlotte Bopp

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# THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'INSTITUT AGRO MONTPELLIER ET DE L'UNIVERSITE DE MONTPELLIER

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École doctorale GAIA

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Centre d'Ecologie fonctionnelle et Evolutive

**Dynamique spatio-temporelle des communautés  
adventices en réponse aux pratiques de gestion des  
sols et conséquences pour les processus de recyclage  
de la matière organique dans les vignobles : une  
approche fonctionnelle**

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# RÉSUMÉ

Les adventices représentent une part importante de la biodiversité végétale spontanée des agroécosystèmes viticoles. Leur gestion sans herbicides constitue un levier majeur de la transition agroécologique. Les objectifs de cette thèse sont (i) **de comprendre la réponse des communautés adventices aux pratiques de gestion du couvert** (désherbage chimique, travail du sol, tonte), **à différentes échelles spatiales et dans le temps**, et (ii) **d'évaluer leurs influences sur les processus de recyclage de la matière organique** (décomposition, activités microbiennes liées au cycle de l'azote), **en utilisant l'approche fonctionnelle**. Pour cela, plusieurs réseaux de parcelles viticoles ont été mobilisés: le réseau national « Biovigilance Flore » qui inclut trois régions viticoles représentant un gradient latitudinal (Champagne, Vallée du Rhône, Languedoc ; 46 parcelles), un réseau régional dans le Bordelais (100 parcelles) et un réseau régional dans le Montpelliérais (40 parcelles), re-mobilisé après 40 ans. Nous démontrons que le changement climatique (+2°C de température estivale) a induit des communautés adventices caractérisées par un score de stress-tolérance 34% plus élevé en 2020s que dans les années 1980s, tandis que la diversification des pratiques de gestion a favorisé des communautés 20% moins compétitives. Les communautés adventices actuelles sont 41 % plus abondantes et 24 % plus riches qu'il y a 40 ans, témoignant d'une certaine résilience face aux changements de pratiques agricoles et climatiques. A grande échelle (nationale), cette thèse démontre que les filtres pédoclimatiques expliquent une plus grande part de variabilité fonctionnelle que les pratiques de gestion des adventices, à l'opposé des résultats à l'échelle régionale. A l'échelle du réseau national Biovigilance, nous démontrons que les communautés adventices issues de parcelles travaillées ont des hauteurs maximales et des capacités de propagation latérale plus élevées que les communautés issues de parcelles désherbées chimiquement. Dans le Bordelais, les communautés issues de parcelles travaillées sont moins compétitives et plus rudérales que les communautés issues de parcelles tondues. Dans le Montpelliérais, le désherbage chimique, appliqué pendant au moins cinq ans, favorise des communautés adventices à stratégie foliaire de conservation des ressources et à potentiel de décomposition 12% plus faible que le travail du sol et la tonte. Les herbicides favorisent des

communautés à stratégies racinaires basées sur l'exploration des ressources du sol tandis que la tonte et le travail du sol sont associés à des communautés adventices dont les stratégies d'acquisition de ressources s'appuient sur la collaboration avec les champignons mycorhiziens. Les communautés adventices à stratégie d'exploration racinaire des ressources du sol sont associées à une plus grande abondance de microorganismes nitrifiants. Cette thèse montre que la pratique de tonte constitue une très bonne alternative à l'usage des herbicides car elle favorise des communautés adventices deux fois plus riches que les autres modes de gestion, qui assurent un meilleur retour de la matière organique au sol grâce à des couverts décomposables, à teneur en azote et biomasse microbienne du sol environ deux fois plus élevées que les autres pratiques. Cette thèse démontre que la gestion des adventices est un puissant levier d'action dans le contexte de la transition agroécologique.

# ABSTRACT

Weed communities constitute an important part of the spontaneous plant biodiversity of vineyards. Their management without herbicides is needed to transition toward agroecology. The objectives of this thesis are (i) **to understand the response of weed communities to management** (chemical weeding, tillage, mowing) **at different spatial scales and over time**, and (ii) **to evaluate their influences on organic matter recycling processes** (decomposition, potential microbial activities related to nitrogen cycle), **using trait-based approach**. Several networks of vineyards were used for this purpose: the national network "Biovigilance Flore" which includes three wine regions representing a latitudinal gradient (Champagne, Rhone Valley, Languedoc; 46 vineyards), a regional network in the Bordeaux region (100 vineyards) and a regional network in the Montpellier region (40 vineyards), re-mobilized after 40 years. From the 1980s to nowadays, climate change (+2°C summer temperature) has induced weed communities characterized by a 34% higher stress-tolerance score, while diversification of management practices has favoured communities that are 20% less competitive. Current weed communities are 41% more abundant and 24% richer than 40 years ago, reflecting their resilience to changes in climate and agricultural practices. At national scale, soil-climate filters explained more functional variability than weed management practices, in contrasts to the results found at regional scales. At the scale of the Biovigilance national network, we showed that weed communities from tilled plots had higher maximum heights and lateral spread capacities than communities from chemically weeded plots. In Bordeaux, communities from tilled plots were less competitive and more ruderal than communities from mowed plots. In the Montpellier region, chemical weed control, applied for at least five years, favoured weed communities with a more resource-conserving foliar strategy and a 12% lower decomposition potential than tillage and mowing. Herbicides promoted root strategies based on soil resource exploration while mowing and tillage were associated with weed communities whose resource acquisition strategies relied on collaboration with mycorrhizal fungi. Weed communities with a root-based resource exploration strategy were associated with a higher abundance of nitrifying microorganisms. This thesis demonstrates that mowing is a very good alternative to the use of

herbicides. After five years, mowing promoted spontaneous covers with high decomposition potential, twice the biomass production and nitrogen content of other management practices, twice the soil microbial biomass of other management practices, and twice the number of weed species. This thesis demonstrates weed management can model more desirable weed communities in the context of the agroecological transition.

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**En 40 ans (des années 1980s à aujourd'hui), le changement climatique (+2°C de température estivale) a induit des communautés adventices plus tolérantes au stress, tandis que la diversification des pratiques de gestion a favorisé des communautés moins compétitives. Les communautés adventices actuelles sont 41 % plus abondantes et 24 % plus riches qu'il y a 40 ans témoignant de leurs résiliences aux changements climatiques et de pratique.**

Bon, ces faits marquants étant établis,

Commençons à remercier.

Mais, avant, peut-être est-il utile de rappeler...

**... Qu'au bout de cinq ans, la tonte favorise des couverts très décomposables, à biomasse et teneur en azote élevées, à biomasse microbienne environ deux fois plus élevée que dans les sols des autres modes de gestion et promeut deux fois plus d'espèces d'adventices que dans les autres modes de gestion.**

Voilà.

Nan, mais c'est important quand même.

A présent que ces résultats qui mèneront à un tournant majeur de l'agroécologie - et plus probablement à une révolution scientifique - sont exposés, il est temps de remercier.

Et je ne commencerai pas par mon chien.



Pour deux raisons principales.

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## SIGLES ET ABBREVIATIONS

**ANOVA** *analysis of variance*

**C** *carbon*

**C:N** *carbon to nitrogen ratio*

**CWM** *community-weighted mean*

**CWV** *community-weighted variance*

**D** *root mean diameter*

**IR** *inter-rang*

**LDMC** *leaf dry matter content*

**Lignine:N** *leaf lignin to nitrogen ratio*

**N** *nitrogen*

**PCA** *principal components analysis*

**PDEA** *potential of denitrifying enzyme activity*

**PNEA** *potential of nitrifying enzyme activity*

**RTD** *root tissue density*

**SIR** *substrate-induced respiration*

**SLA** *specific leaf area*

**SOM** *soil organic matter*

**SRL** *specific root length*





# INTRODUCTION



Communautés adventices selon Tatiana Cardenas (Equateur, novembre 2022)



# 1. Agriculture et biodiversité

En 1992, le Sommet de la Terre à Rio lance de nouvelles réflexions sur les liens entre agriculture et biodiversité et sur la multifonctionnalité de l'agriculture (Le Roux et al., 2008). Les réflexions sur les relations agriculture-biodiversité aboutissent au concept d'**agrobiodiversité**, c'est-à-dire la variabilité des organismes vivants qui contribuent à l'alimentation et à l'agriculture, ainsi qu'aux connaissances associées à elles (Pautasso et al., 2013). L'agrobiodiversité regroupe la biodiversité dite « planifiée », volontairement introduite par les agriculteurs et agricultrices comme la diversité génétique des plantes cultivées (Khoury et al., 2022) mais aussi la biodiversité associée comme les adventices des cultures (Spahillari et al., 1999). A l'image de la biodiversité dite « sauvage », l'agrobiodiversité s'érode drastiquement: la FAO estime que 75% de l'agrobiodiversité aurait disparu depuis les années 1990 (FAO, 2010). La deuxième réflexion que lance le Sommet de Rio s'axe sur la **multifonctionnalité de l'agriculture**, c'est-à-dire, l'idée que l'agriculture produit à la fois de la nourriture et des fibres, mais peut préserver aussi les habitats, les paysages, développe les territoires ruraux... (Le Roux et al., 2008). En réponse aux réflexions sur l'agrobiodiversité et la multifonctionnalité de l'agriculture, initiées à Rio, le concept d'agroécologie ainsi que de 'transition agroécologique' s'étendent largement. L'agroécologie s'appuie sur l'application des concepts et principes de l'écologie à la conception et à la gestion d'agroécosystèmes<sup>1</sup> durables (Gliessman, 1998), notamment *via* la réintroduction de la biodiversité dans l'espace (*e.g.* mélanges variétaux) et dans le temps (*e.g.* rotations de cultures) (Altieri and Francis, 1992). L'identification et l'adoption de pratiques agricoles favorisant une biodiversité planifiée ou associée au sein des agroécosystèmes est l'un des piliers de la transition agroécologique (Dumont et al., 2021).

**Les adventices**, communément appelées 'mauvaises herbes', **représentent une composante majeure de l'agrobiodiversité végétale spontanée associée** (Marshall et al., 2003; Petit et al.,

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<sup>1</sup> Un agroécosystème est un écosystème géré dans l'intention de produire, distribuer et consommer de la nourriture, des combustibles, des fibres et d'autres ressources, infrastructures, marchés, institutions et les personnes engagées dans ces fonctions (Duru et al., 2015).

2018, 2011): 1402 espèces d'adventices ont été répertoriées en France (Munoz et al., 2020), soit 23% des espèces végétales françaises (INPN, 2022). Les agroécosystèmes pérennes (*e.g.* vergers, vignes) sont caractérisés par une grande disponibilité d'espace pour les adventices par rapport aux cultures annuelles, plus densément semées. Ces deux dernières décennies, les viticulteurs et viticulteurs ont diversifié leurs pratiques de gestion des adventices (Winter et al., 2018) et peu d'études ont encore étudié la réponse des communautés adventices à ces nouvelles combinaisons de pratiques, notamment dans les agroécosystèmes méditerranéens hébergeant la plus grande part de diversité en adventices en France (Munoz et al., 2020). **L'identification de pratiques de gestion des couverts spontanés<sup>2</sup>** favorisant des communautés adventices diversifiées et multifonctionnelles dans différents contextes pédoclimatiques est déterminante pour favoriser des agroécosystèmes plus durables. Une meilleure compréhension de **l'influence des adventices sur les processus des agroécosystèmes viticoles** est majeure pour piloter des pratiques de gestion maximisant leur multifonctionnalité. **Les communautés adventices des vignobles français constituent l'objet d'étude central de la thèse.**

## 2. Qu'est-ce qu'une adventice ?

### 2.1. Une définition anthropocentrée et non consensuelle

« *Any article which purports to deal with weeds should begin with definitions of 'weed' and 'weedy'* ». Baker, 1965, *Characteristics and Modes of Origin of Weeds*

Les définitions du terme « *adventice* » sont nombreuses et encore débattues (Zimdahl, 2018). En français, le terme plus commun de « *mauvaises herbes* » revêt une connotation négative, tout comme en espagnol « *mala hierba* », en italien « *malherbe* » ou en grec « *zizania* » (d'où vient d'ailleurs l'expression « *semer la zizanie* »). C'est au XVIII<sup>ème</sup> siècle qu'apparaît le terme plus neutre « *adventice* », emprunté à la philosophie. En français, l'étymologie « *adventice* » vient du latin

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<sup>2</sup> Dans la thèse, l'utilisation de « *couvert* » ou « *couvert spontané* » est synonyme de « *communautés adventices* ».

« *adventicius* », c'est-à-dire, « *ce qui vient du dehors, étranger* » (CNRTL, 2022). La première définition du terme « *adventice* » est donnée en 1776 par Schabol: « *celles qui croissent sans avoir été semées* ». Quelques siècles plus tard, la *Weed Science Society of America* définit les adventices comme « *toute plante poussant là où elle n'est pas désirée* » (Buchholtz, 1967) tandis que l' *European Weed Research Society* les définit comme « *toute plante ou végétation à l'exception des champignons, qui interfère avec les objectifs et les besoins humains* » (Vencill, 2022) (Figure 1). D'autres définitions moins officielles interrogent la perception négative associée au terme plus commun « *mauvaises herbes* », comme celles de botanistes amateurs: « *Qu'est-ce donc qu'une mauvaise herbe, sinon une plante dont on n'a pas encore découvert les vertus ?* » (Emerson, 1912), des plantes « *condamnées sans un procès équitable* » (King, 1951) ou encore celles d'artistes: « *La mauvaise herbe n'est jamais qu'une fleur mal aimée* » (Ella Wheeler Wilcox) (Figure 1). Finalement, ces définitions interrogent la subjectivité des définitions officielles. Indésirables pour qui et pour quel objectif ? Pour des vigneronnes et vigneronnes de mon entourage et du réseau de parcelles viticoles de la thèse, « *Les adventices sont les plantes concurrentes à la vigne et à la production de raisins* » ou encore, avec une pointe d'humour: « *Les adventices sont les plantes néfastes à la santé des vignes. Et qui piquent aux pieds.* » (Figure 1). Pour une jardinière, ce sont « *des plantes qui ne sont pas jolies* ». Pour un célèbre chanteur anarchiste, des « *rebelles et marginales* » (Figure 1)... Très récemment, Merfield (2022) propose une nouvelle définition « *post-herbicide* » du terme: « *Une plante, ou une population de plantes, à un moment et dans un lieu spécifique, causant un préjudice important, soit immédiatement, soit à plus long terme, sur la base d'une analyse holistique de leurs attributs positifs et négatifs.* ». Ainsi, les plantes sont définies comme « *adventices* » au cas par cas, après une évaluation complète des effets négatifs et positifs qu'elles ont sur tout écosystème. **Dans la suite de la thèse, nous considérerons les adventices comme toute espèce végétale spontanée (non semée), désirable ou non, située au sein des parcelles cultivées.**

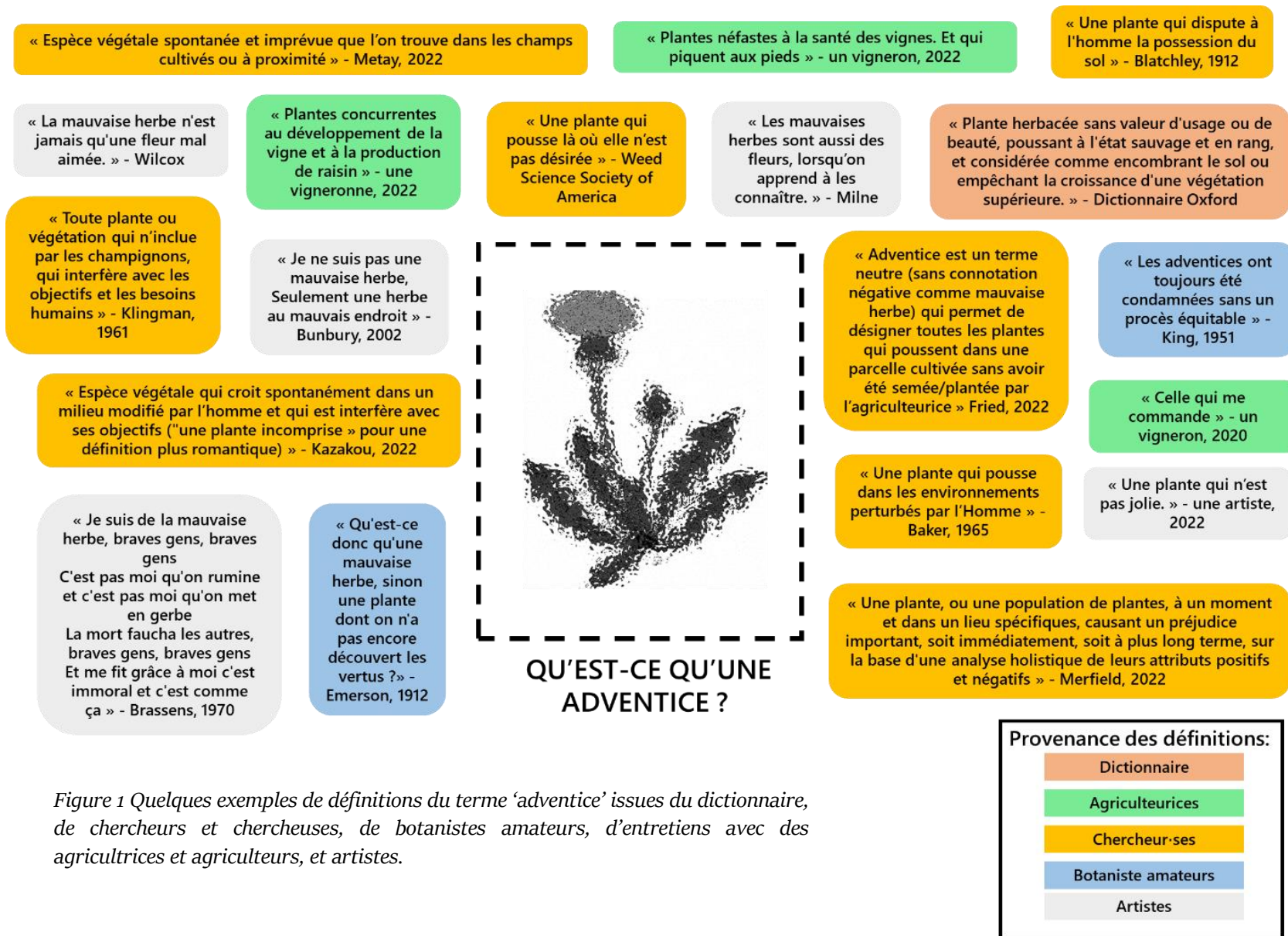


Figure 1 Quelques exemples de définitions du terme 'adventice' issues du dictionnaire, de chercheurs et chercheuses, de botanistes amateurs, d'entretiens avec des agricultrices et agriculteurs, et artistes.

## 2.2. D'où viennent les adventices ?

Contrairement à l'étymologie « *adventicius* » qui suggère que les plantes adventices se sont introduites dans les cultures, les premières adventices parmi lesquelles, le chiendent rampant (*Elymus repens*), la stellaire intermédiaire (*Stellaria media*) ou le gaillet gratteron (*Galium aparine*) étaient bien présentes en Europe occidentale avant l'apparition de l'agriculture<sup>3</sup> (Figure 2). A l'origine, les adventices sont les espèces pionnières ayant colonisé les milieux ouverts et/ou naturellement perturbés (berges de rivières, micro perturbations dans les prairies par les grands mammifères) avant que la forêt ne domine le paysage, après la dernière ère glaciaire (Figure 2). L'analyse des diagrammes polliniques permet de retracer leurs dates de colonisation, comme dans l'exemple présenté sur la Figure 2 au Mont d'Aubrac (Pons et al., 1990). Au fil des siècles après l'apparition de l'agriculture, les adventices dites « archéophytes » se sont introduites dans les champs cultivés jusqu'au début du XVIème siècle (Chauvel et al., 2018): par exemple, le coquelicot (*Papaver rhoeas*) ou le gaillet à trois cornes (*Galium tricornutum*). Les espèces adventices introduites ultérieurement à ce siècle sont appelées « néophytes » et proviennent majoritairement des Amériques: par exemple, la vergerette du Canada (*Erigeron canadensis*) ou l'amarante réfléchie (*Amaranthus retroflexus*) (Figure 2).

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<sup>3</sup> Devrait-on appeler les cultures, des 'adventices', dans ce cas ?

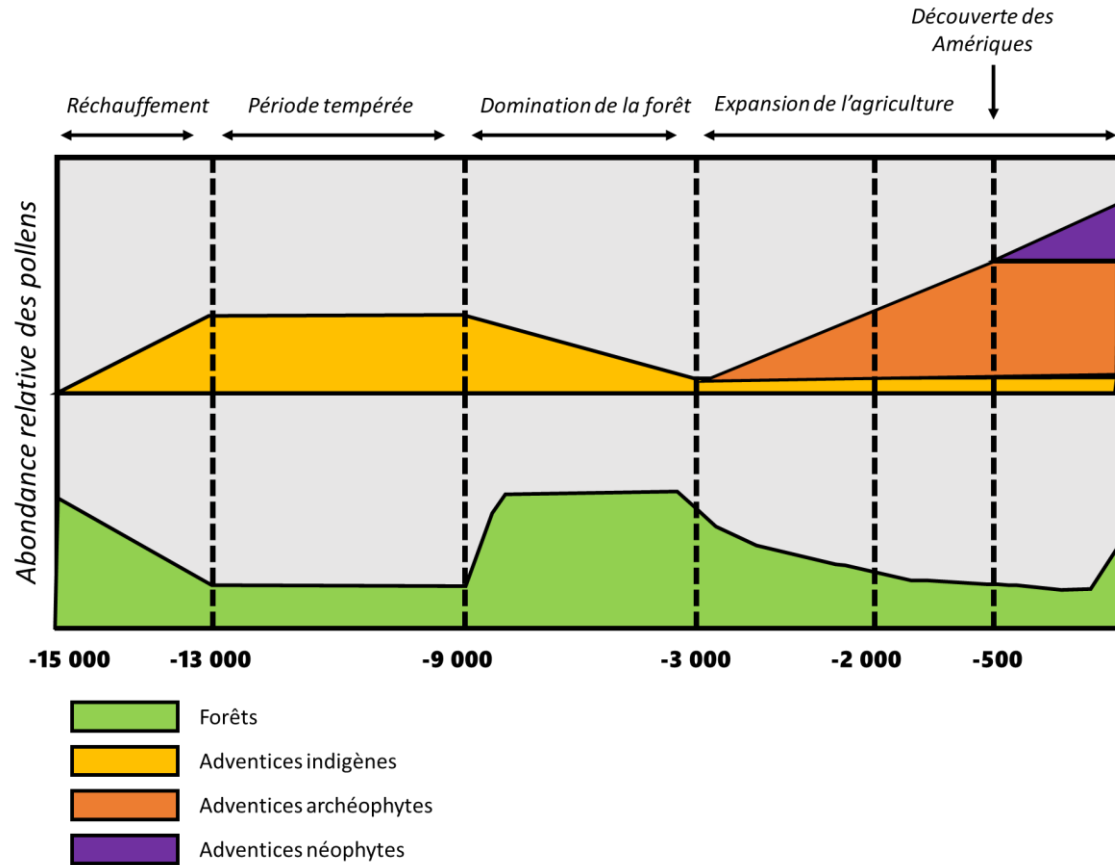


Figure 2 Représentation très schématique d'un diagramme pollinique constitué au Mont d'Aubrac par Pons (1990). Le réchauffement de -15 000 à -13 000 ans puis la période tempérée de -13 000 à -9 000 ans créent des conditions favorables à l'expansion des premières adventices indigènes héliophiles. A partir de -9 000, la forêt referme les milieux précédemment ouverts par la déglaciation et l'abondance pollinique des premières adventices diminue. En -3 000, les premiers pollens de céréales cultivées sont retrouvés. L'agriculture ouvre les milieux et favorise de nouvelles espèces adventices appelées archéophytes, en plus des espèces indigènes. Au XV<sup>ème</sup> siècle, les Amériques sont découvertes et les cultures importées enrichissent le pool d'espèces adventices européen. Les adventices introduites après 1 500 sont appelées les néophytes.



## 2.3. Quelle définition fonctionnelle pour les adventices ?

### 2.3.1. De l'approche taxonomique à l'approche fonctionnelle: du nom latin à la mesure de « *traits* »

L'approche fonctionnelle considère une espèce, non pas sous l'angle de son identité et de son nom latin, mais sous l'angle de ses « *traits fonctionnels* » (Garnier et al., 2016) (Box 1). Les traits fonctionnels sont définis comme les caractéristiques morphologiques, physiologiques ou phénologiques mesurables à l'échelle de l'individu qui affectent la fitness *via* leurs effets sur la croissance, la reproduction et la survie (Violle et al., 2007). Une grande variabilité de traits fonctionnels a été décrite, permettant de caractériser de nombreuses fonctions des plantes comme la dispersion des graines (masse des graines), la photosynthèse (teneur en azote foliaire qui renseigne de la concentration en protéines RubisCO) ou l'exploration souterraine des racines (longueur spécifique racinaire définie comme le ratio entre la longueur des racines et leurs masses sèches) (Pérez-Harguindeguy et al., 2016).

**Box 1** Caractérisation d'un ou d'une élève de classe par analogie à une adventice en utilisant l'approche taxonomique et fonctionnelle. L'approche taxonomique consiste à identifier et nommer l'élève, tandis que l'approche fonctionnelle se base sur la mesure de certains traits liés à la valeur sélective de l'élève (sa taille, son poids et si Camille a tendance à végéter l'après-midi).

#### **APPROCHE TAXONOMIQUE**

Prénom NOM  
Camille DIOU



#### **APPROCHE FONCTIONNELLE**

Taille  
1m34

Poids  
48 kg

Végète l'après-midi  
Oui

### 2.3.2. Les adventices ont-elles des valeurs de traits spécifiques ?

En 1965, Baker définit les adventices comme « toute espèce adaptée aux milieux perturbés ». Une perturbation est « tout événement relativement discret dans le temps qui perturbe la structure de l'écosystème, de la communauté ou de la population et modifie les ressources, la disponibilité du substrat ou l'environnement physique » (White and Pickett, 1985) ou encore « tous les mécanismes qui limitent la biomasse des plante en causant leurs destructions » (Grime, 1977). En milieu agricole, les pratiques de gestion des adventices comme le travail du sol ou le désherbage chimique sont des exemples de perturbation car elles détruisent ponctuellement la biomasse adventice (Gaba et al., 2014; Kazakou et al., 2016). Baker propose une première liste de caractéristiques que présenterait « l'adventice idéale » (Tableau 1): par exemple, la production de nombreuses graines à longue longévité, une croissance rapide, une grande capacité de dispersion...

Tableau 1 Les caractéristiques 'idéales' des adventices selon Baker (1965)

Caractéristiques des adventices « idéales »
1. Absence d'exigences environnementales particulières pour la germination
2. Germination discontinue et longue longévité des graines
3. Croissance rapide des plantules
4. Courte période végétative avant la floraison
5. Maintien d'une production de graines continue tant que les conditions le permettent
6. Autogame
7. Si la pollinisation est croisée, elle peut être faite par un pollinisateur non spécialiste ou par le vent
8. Production de nombreuses graines quand les conditions sont favorables
9. Capacité à produire des graines dans une large gamme de conditions environnementales (souvent une grande plasticité)
10. Capable de disperser à la fois à grande et petite distance
11. S'il s'agit d'une pérenne, présente une reproduction végétative vigoureuse
12. S'il s'agit d'une pérenne, présente une fragilité au niveau des nœuds inférieurs ou des rhizomes ou stolons
13. S'il s'agit d'une pérenne, capacité à se régénérer à partir d'une portion de stolons

En 1974, Grime définit des stratégies<sup>4</sup> que les espèces végétales peuvent mettre en place pour s'adapter aux deux contraintes environnementales suivantes: (i) le stress, relié au manque de

<sup>4</sup> Le terme "stratégie" fait référence aux moyens employés par une espèce pour maintenir sa population dans un écosystème (Westoby, 1998).

ressources (par exemple, l'eau ou l'azote) et (ii) la présence de perturbations. Trois stratégies sont possibles: (i) la stratégie « *stress-tolérance* » dans les habitats pauvres en ressources et peu perturbés, (ii) la stratégie « *rudérale* » dans les environnements perturbés et riches en ressources et (iii) la stratégie « *compétitive* » dans les habitats les plus riches en ressources et peu perturbés (Figure 3). Selon ce schéma, les adventices sont classées comme espèces rudérales, adaptées aux milieux perturbés par les pratiques agricoles.

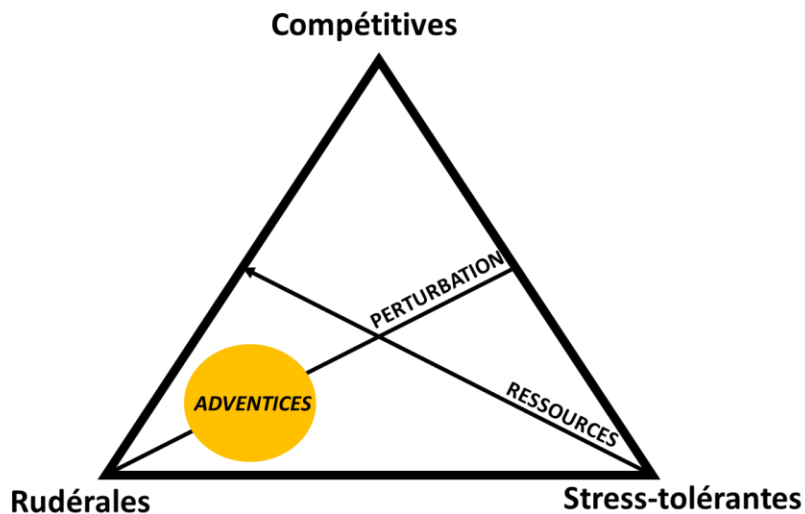


Figure 3 Triangle « CSR » élaboré par Grime (1974, 1977) qui décrit les trois stratégies suivantes: (i) les espèces végétales stress-tolérantes dans les habitats pauvres en ressources et peu perturbés, (ii) les espèces végétales rudérales dans les environnements perturbés et riches en ressources et (iii) les espèces végétales compétitives dans les habitats les plus riches en ressources et peu perturbés. Selon la définition de Baker (1965) et Grime (1977), les adventices sont des espèces rudérales (représentées par le rond jaune sur la figure).

Grime associe la stratégie « *rudérale* » aux valeurs de traits suivantes, dont certaines sont similaires à celles présentes dans la liste de Baker : une hauteur faible, un taux de croissance relatif maximale potentielle élevé, une courte longévité des feuilles et une forte production de petites graines. Cette stratégie dite « *acquisitive* » consiste à maximiser la photosynthèse tout en réduisant l'investissement dans les organes photosynthétiques, à faible durée de vie. Les espèces acquiesitives ont un retour sur investissement en nutriments et en masse sèche élevé (Wright et al., 2005). Au contraire, la stratégie « *conservative* » est associée à un taux d'acquisition de carbone plus lent, des

feuilles résistantes à longue durée de vie et à un faible retour sur investissement. Un trait classique en écologie fonctionnelle renseigne cette stratégie: la surface foliaire spécifique (*specific leaf area*, SLA) (Box 3). La surface foliaire spécifique est le ratio entre la surface d'une feuille et sa masse sèche. Les adventices à SLA élevé ont de larges surfaces photosynthétiques pour de faibles masses sèches foliaires (c'est le cas de *Setaria viridis*). Au contraire, les adventices à SLA faibles ont de plus petite surface photosynthétique par unité de matière sèche investie et ont une stratégie de conservation de ressources (c'est le cas de *Cirsium arvense*) (Box 3).

**Box 2 La surface foliaire spécifique (i.e. le ratio entre la surface d'une feuille et sa masse sèche) renseigne la stratégie des adventices.** Si on assimile une feuille à un panneau solaire, une plante à SLA élevé (« *Specific Leaf Area* » en anglais) investit dans des panneaux solaires bon marché, à efficacité élevée par rapport au prix d'investissement, mais peu durables dans le temps. C'est cette stratégie acquisitive qu'utilise *Setaria viridis* par exemple. Au contraire, les adventices à faible SLA, comme *Cirsium arvense*, investissent dans des panneaux solaires onéreux et robustes, et durables mais qui sont peu efficaces par rapport au prix initial investi sur le court terme.

**SLA faible**  
Investissement élevé  
Faible efficacité par €  
Longue durée de vie



Ex : *Cirsium arvense*



**SLA élevée**  
Investissement faible  
Efficacité élevée par €  
Faible durée de vie



Ex : *Setaria viridis*



# 3. D'une adventice à plusieurs: comment les adventices s'assemblent-elles en communautés ?

## 3.1. La théorie des filtres environnementaux

En écologie, une communauté est un groupe d'espèces qui partage un même espace, au même moment (Begon et al., 1990). **Dans le cadre de cette thèse, nous considérons qu'une communauté adventice est l'ensemble des adventices présentes sur une zone délimitée d'une parcelle viticole variant de 60x60 cm<sup>2</sup> à 2000 m<sup>2</sup> selon les chapitres de thèse.** Comprendre comment des espèces s'assemblent au sein des communautés est l'une des questions fondamentales de l'écologie des communautés (Lavorel and Garnier, 2002). Deux grands types de théories ont émergé en réponse à cette question: la théorie neutre, basée sur des processus stochastiques, et les théories de niches, basées sur des processus déterministes (Figure 4). La théorie neutre de Hubbell (2001) assume que tous les individus d'une communauté ont la même probabilité de se reproduire ou de mourir. Cela suppose que les espèces appartenant à la même communauté sont fonctionnellement équivalentes (Figure 4). Selon la théorie neutre, l'assemblage des communautés est aussi gouverné par des processus stochastiques comme la contingence historique (l'ordre d'arrivée des espèces) ou la limite de dispersion. Au contraire, les théories de niche supposent que l'assemblage des communautés n'est pas aléatoire et est gouverné par des processus déterministes, tels que les filtres environnementaux, le partitionnement de niches, la hiérarchie de compétition entre les espèces. Il est à présent admis que les deux types de processus structurent l'assemblage des communautés et que leurs poids respectifs est variable suivant l'échelle d'étude et les habitats.

La Théorie des Filtres énoncée par Keddy (1992) définit les règles d'assemblage d'une communauté selon une série hiérarchisée de filtres de différentes natures sélectionnant graduellement les espèces au sein de différents pools en fonction de leurs valeurs de traits (Figure 5). Le premier pool global est constitué de l'ensemble des espèces qui existent sur Terre. Un premier filtre stochastique de dispersion sélectionne les espèces capables de disperser à l'échelle régionale

pour former le « *pool d'espèces régional* » (Garnier et al., 2016): c'est-à-dire toutes les espèces ayant des valeurs de traits

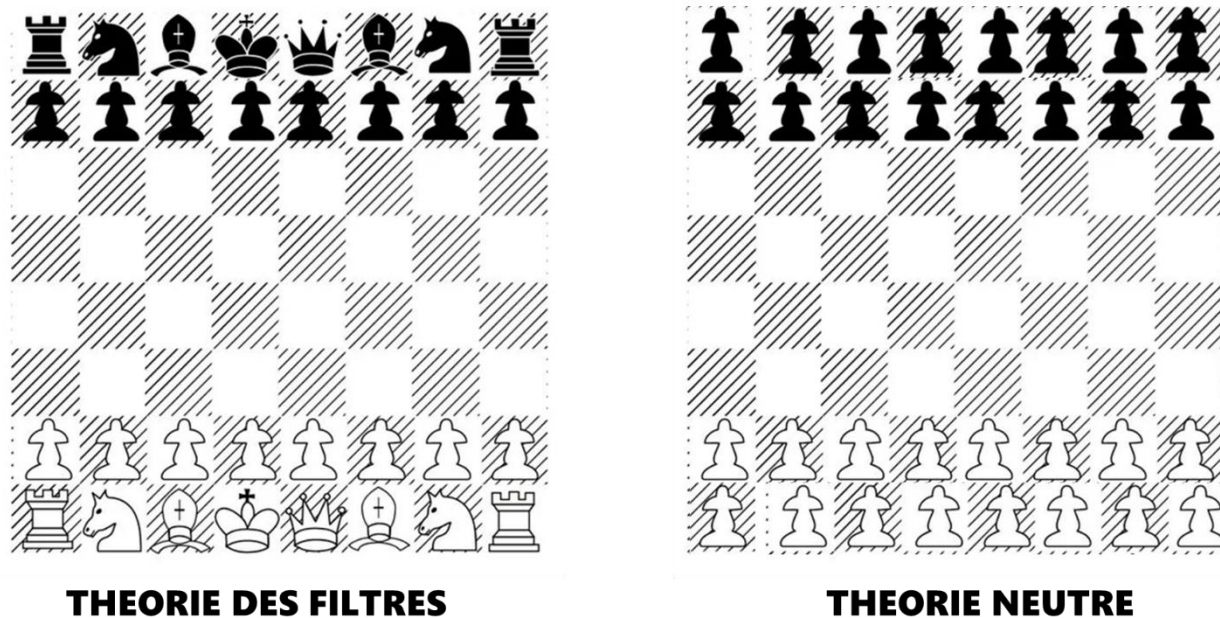


Figure 4 Comparaison de la théorie des filtres (et de niche plus généralement) et la théorie neutre. La théorie neutre considère que les espèces appartenant à la même communauté sont fonctionnellement équivalentes. Si l'on prend l'image d'un jeu d'échec constitué de l'ensemble des pièces classiques (à gauche de la figure), représentant des espèces différentes au sein d'une communauté, celles-ci sont caractérisées par une aptitude à se déplacer différemment dans l'espace (le fou en diagonal, le pion, d'une seule case). Selon la théorie des filtres, certaines espèces sont favorisées par leurs capacités intrinsèques à survivre dans un environnement donné. Les pièces de l'échiquier restantes à la fin du jeu le sont notamment dû à leurs capacités à se déplacer qui leur confèrent un avantage pour ne pas être éliminées. Selon la théorie neutre, toutes les pièces ont les mêmes capacités à survivre dans un environnement et sont toutes des pions. A la fin du jeu, les pièces restantes le sont dû à des facteurs externes (l'ingéniosité de l'adversaire par exemple) et indépendants de leurs façons de se déplacer.

adaptées ; les autres espèces ne pouvant pas persister. A l'échelle locale, les espèces sont filtrées par des filtres abiotiques. Ces filtres sélectionnent les espèces capables de tolérer les conditions du milieu (Garnier et al., 2016): les caractéristiques du sol (e.g. pH, matière organique), du climat (e.g. température, précipitation), les ressources disponibles (e.g. lumière, azote) et le régime de perturbation (e.g. incendie, inondations). Par exemple, Bernard-Verdier et al. (2012) démontre que les espèces prairiales à valeurs de SLA faibles et à stratégie conservative étaient favorisées sur sols peu profonds tandis que les espèces à valeurs de SLA élevée et à stratégie plus acquisitive se développaient mieux sur sols profonds. Le filtre biotique correspond aux interactions positives et

négligentes existant entre les espèces d'une même communauté: compétition, facilitation, herbivorie, parasitisme. Par exemple, Luzuriaga et al. (2012) ont démontré que la présence d'une espèce pérenne favorisait la présence des espèces annuelles dans des milieux semi-arides en créant des zones de refuge aux microclimats plus doux. Booth & Swanton (2002) adaptent la théorie des filtres au contexte des adventices en milieu agricole, et prennent formellement en compte les facteurs anthropiques.

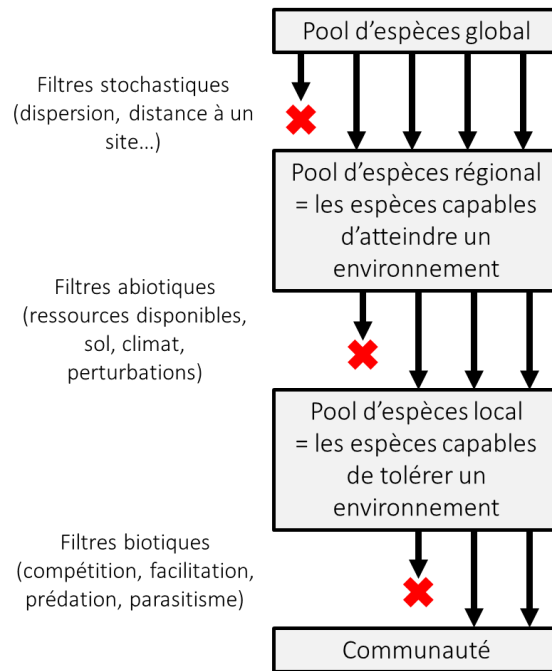


Figure 5 Les règles d'assemblage des communautés selon la Théorie des Filtres (Keddy, 1992). Ce graphique est inspiré de Garnier et al. (2016), Lortie et al. (2004) et de Fried (2019).

## 3.2. Les filtres agro-environnementaux des communautés adventices

Bien que cette thèse se base sur différents bassins viticoles, la plupart des travaux de thèse ont été effectués dans des vignobles méditerranéens (chapitre 3, 4, 5 ; Figure 16). La Figure 6 synthétise les filtres majeurs auxquels sont soumis ces communautés en lien avec le climat, le sol et les pratiques

viticoles, notamment celles liées à l'entretien du sol. Dans la suite de la thèse, nous qualifions l'ensemble de ces filtres de « *filtres agro-environnementaux* ».

### 3.2.1. Les filtres pédoclimatiques des communautés adventices des vignobles méditerranéens

Le climat méditerranéen semi-aride constitue l'un des premiers filtres abiotiques avec des températures annuelles élevées, précipitations irrégulières et un indice d'aridité faible<sup>5</sup> (Figure 6).

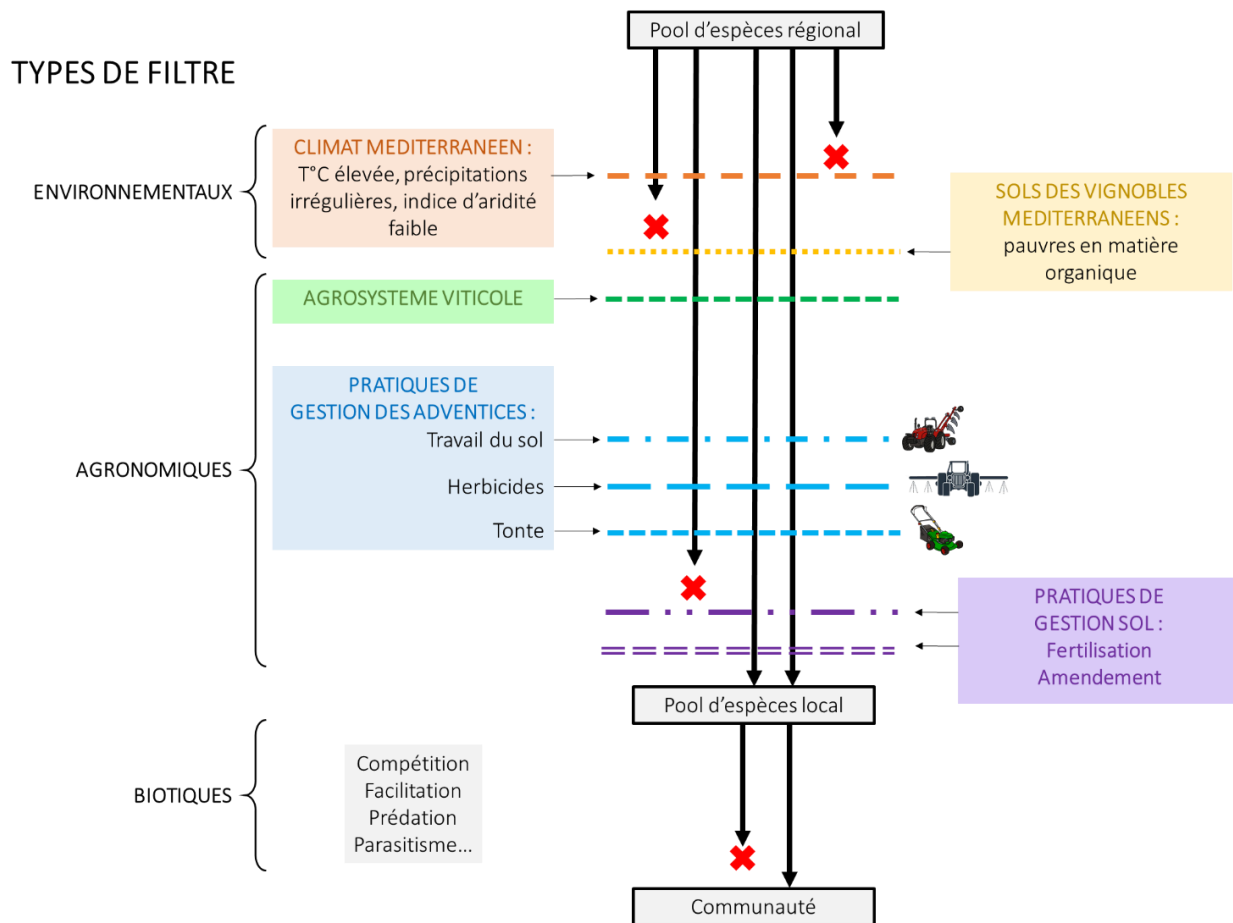


Figure 6 Les filtres abiotiques et biotiques des communautés adventices des vignobles méditerranéens.

En milieu semi-aride, les espèces ont plutôt des stratégies de conservation de ressources (masse de graines élevée, SLA plus faible, teneur en matière sèche foliaire<sup>6</sup> plus élevée, teneur en azote foliaire

<sup>5</sup> L'indice d'aridité est le rapport précipitation sur évapotranspiration. Plus l'indice est faible, plus le climat est aride.

<sup>6</sup> La teneur en matière sèche foliaire est le ratio entre la masse sèche et la masse fraîche des feuilles



plus faible) (Garnier et al., 2019). Les sols des agroécosystèmes viticoles méditerranéens sont pauvres en matière organique et soumis à des risques accrus d'érosion (Novara et al., 2018; Romero et al., 2022) (Figure 6). Les sols peu fertiles sont également associés avec des communautés à stratégie de conservation des ressources (Wardle et al., 2004).

### **3.2.2. Les filtres agronomiques des communautés adventices dans les agroécosystèmes viticoles**

Le type de culture ainsi que la succession de cultures constituent un premier filtre lié à la disponibilité de l'habitat entre le semis et la récolte (Figure 6). Par exemple, Mahaut et al. (2018) ont démontré que la diversité des communautés adventices augmente avec la variabilité de la date de semis des cultures de plusieurs rotations. Les agroécosystèmes viticoles sont moins densément plantés que les agroécosystèmes annuels et offrent une plus grande disponibilité spatiale, notamment au sein des inter-rangs (*i.e.* espace 'libre' entre les rangées de vigne) (Figure 7). Dans les vignobles, trois pratiques de gestion des adventices sont mises en place et constituent des filtres anthropiques additionnels: le désherbage chimique, le travail du sol et la tonte (Figure 6, Figure 7) (Fernández-Mena et al., 2021). Ces types de gestion peuvent être combinés sur des inter-rangs différents au sein d'une même parcelle (ce qui est le cas sur la Figure 7), ou même sur un même inter-rang à différentes périodes (par exemple, un premier désherbage chimique en mars et une tonte en juin) (Box 3). Ces trois pratiques sélectionnent des communautés adventices différentes, parfois visibles à l'œil nu sur le terrain, comme par exemple, la présence de *Diplotaxis erucoïdes*, favorisée par le travail du sol (fleurs blanches sur la Figure 7). Les pratiques de gestion des adventices constituent des perturbations différentes pour le sol et pour les communautés végétales de par leurs intensités (quantité de biomasse détruite) et leurs fréquences (temps entre chaque perturbation) (Gaba et al., 2014; Guerra et al., 2022) mais aussi de par le mécanisme de destruction (arrêt de la photosynthèse provoqué par le glyphosate, arrachage de la plante entière par le travail du sol). Le travail du sol et le désherbage chimique détruisent entièrement la biomasse d'adventice tandis que la tonte l'enlève partiellement. **Ainsi, nous posons l'hypothèse que le travail du sol et le désherbage chimique constituent des perturbations plus intenses que la tonte (Figure 8). De plus, les couverts tondu étant plus denses (car non détruits entièrement), nous faisons l'hypothèse que la**

compétition doit être plus intense dans les vignobles tondus que dans les vignobles désherbés et travaillés (Figure 8). Ainsi, nous posons l'hypothèse que les communautés adventices issues de parcelles travaillées et désherbées chimiquement ont une stratégie plus rudérale que les communautés issues de parcelles tondues qui ont une stratégie plus compétitive (Figure 8).

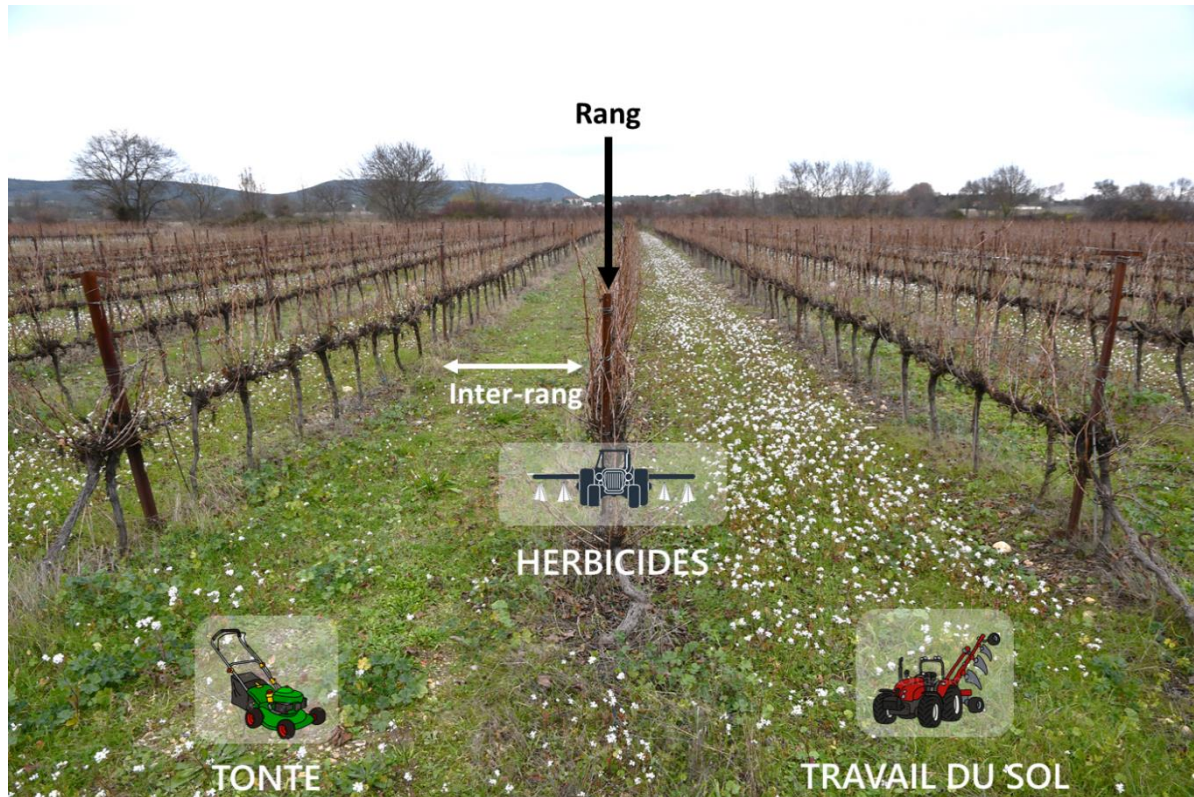
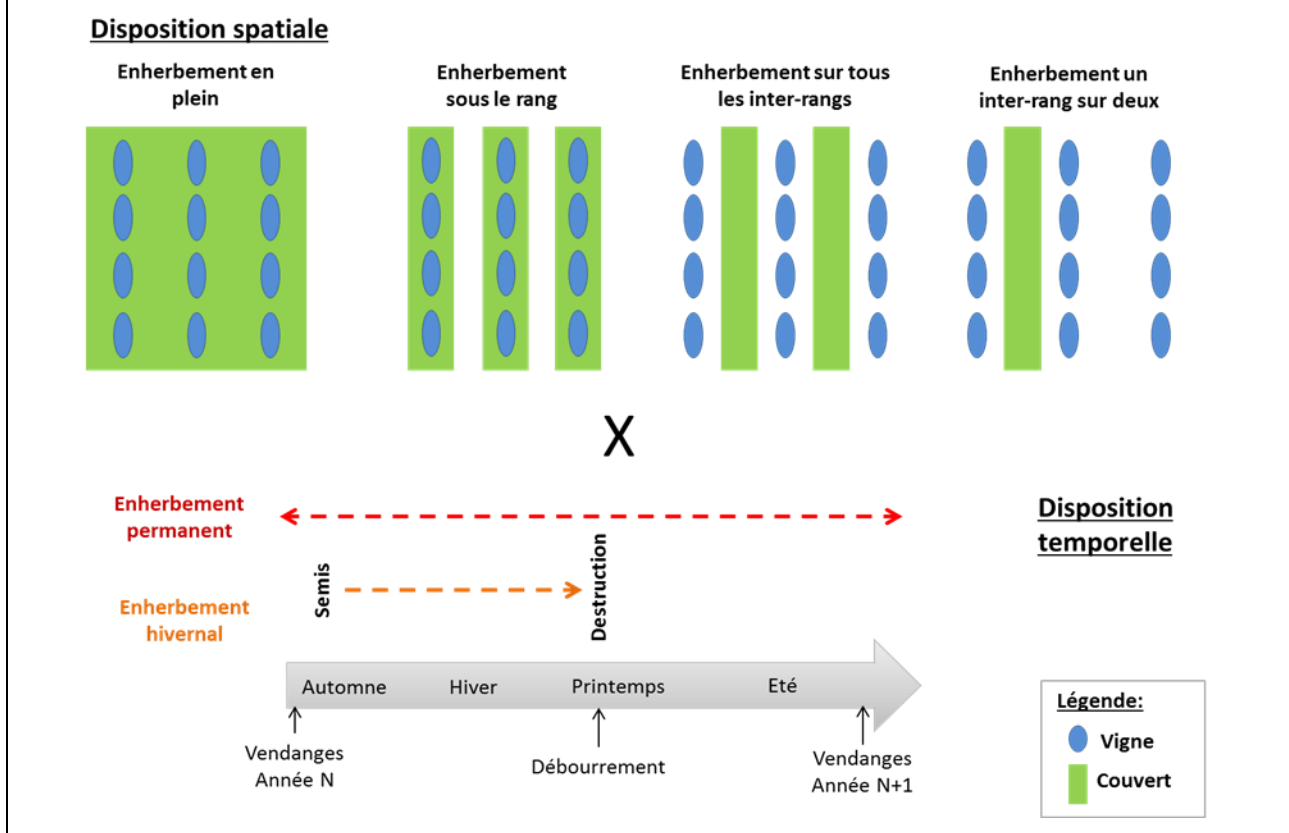


Figure 7 Les trois pratiques de gestion des adventices appliquées en viticulture. Le rang de vigne est désherbé chimiquement. L'inter-rang à gauche sur la photo (i.e. l'espace disponible entre deux rangées de vigne) est tondu. L'inter-rang de droite est travaillé. Les fleurs blanches (*Diplotaxis erucoides*), abondantes dans l'inter-rang de droite, sont favorisée par le travail du sol. Cette photo illustre bien les différents filtres que constituent les différentes pratiques de gestion dont les effets sur la composition floristique sont détectables à l'œil nu. Photo prise par Guillaume Fried, dans une parcelle du réseau Montpellierais, dans l'Hérault.

De récentes études sur la flore des vignobles ont montré que la tonte favorise les communautés adventices à stratégie de conservation de ressources par rapport à d'autres pratiques (Guerra et al., 2021; Hall et al., 2020; Kazakou et al., 2016; Mainardis et al., 2020): masse de graines et hauteur plus élevées, plus faible SLA et teneur en matière sèche des feuilles plus élevée, espèces pérennes plus abondantes. Au contraire, le travail du sol et le désherbage chimique sélectionnent des

communautés plus acquiescentes, composées de plus d'annuelles et d'espèces fleurissant plus tardivement, à SLA plus élevée et teneur en matière sèche foliaire plus faible (Hall et al., 2020).

**Box 3 Les différentes dispositions spatio-temporelles des couverts spontanés des agroécosystèmes viticoles.** Une grande variabilité de dispositions spatiales et temporelles existe pour l'enherbement dans les agroécosystèmes viticoles. L'enherbement peut être présent sur la totalité de la surface de la parcelle (« enherbement en plein »), sous le rang de vigne et détruit dans l'inter-rang, détruit sous le rang de vigne et conservé dans l'inter-rang et peut uniquement être conservé un inter-rang sur deux, trois et parfois quatre. L'enherbement peut également être conservé toute l'année (enherbement permanent) et géré par des tontes, sans destruction totale par désherbage chimique ou travail du sol. Le couvert spontané peut être détruit plusieurs fois dans l'année, souvent à partir du printemps lorsque la vigne débourre et que ses besoins hydriques et azotés augmentent (Garcia et al., 2018).



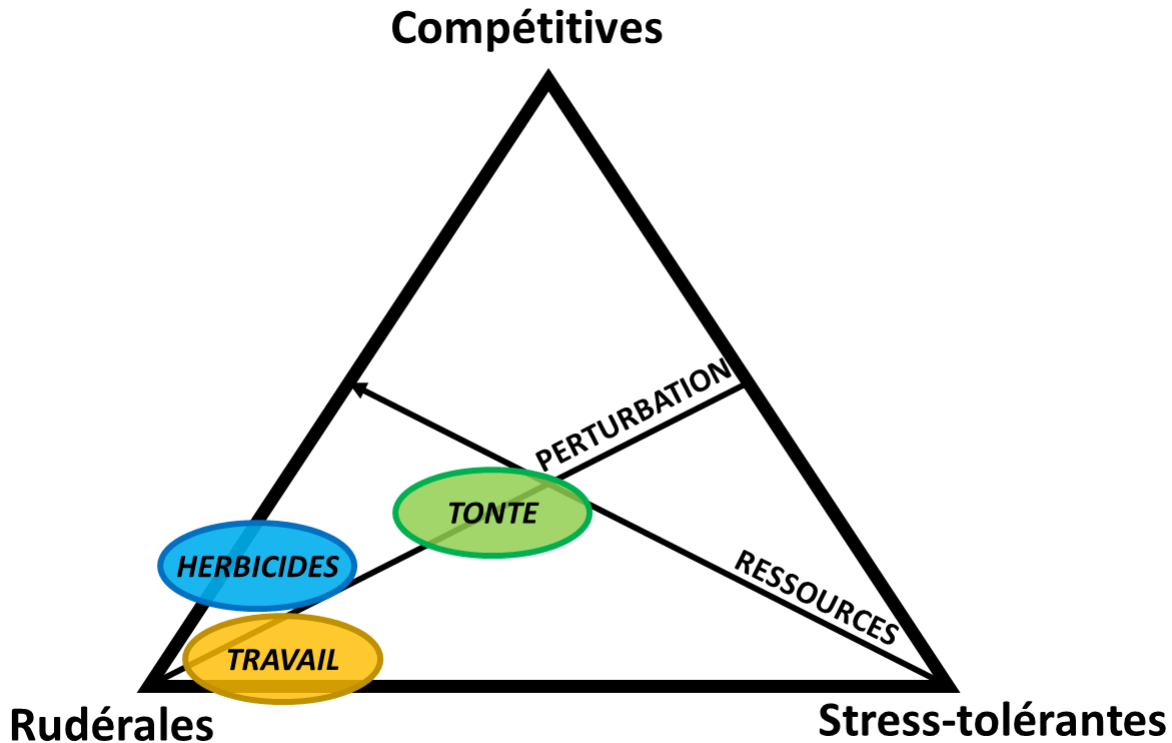


Figure 8 Hypothèses des effets des pratiques de gestion des adventices sur les stratégies CSR des communautés adventices. Ces trois pratiques constituent des perturbations différentes de par leurs intensités (quantité de biomasse détruite) et leurs fréquences (temps entre chaque perturbation) mais aussi de par le mécanisme de destruction (arrêt de la photosynthèse provoqué par le glyphosate, arrachage de la plante entière par le travail du sol). Le travail du sol et le désherbage chimique détruisent entièrement la biomasse d'adventice tandis que la tonte l'enlève partiellement. Ainsi, nous posons l'hypothèse sur le travail du sol et le désherbage chimique constituent des perturbations plus intenses que la tonte.

### 3.2.3. Les changements temporels de filtres agronomiques et environnementaux dans les agroécosystèmes viticoles

Les filtres agronomiques (e.g. les pratiques de gestion du sol) et environnementaux (e.g. le climat) peuvent évoluer au cours du temps et favoriser des stratégies différentes chez les communautés adventices.

### 3.2.3.1. *Caractéristiques du changement climatique et effet sur les communautés adventices*

Le changement climatique résulte en une hausse des températures, des précipitations altérées (et qui diminuent dans le cas du pourtour méditerranéen), une fréquence accrue d'événements climatiques extrêmes et une augmentation de la pression de CO<sub>2</sub> dans l'atmosphère (Peters et al., 2014). Peu d'études se sont intéressées à l'impact du changement climatique sur les communautés adventices, d'un point de vue fonctionnel. Clements & Ditommaso (2011) dressent les propriétés fonctionnelles nécessaires à l'adaptation des adventices et des espèces invasives aux nouvelles conditions climatiques (Tableau 2). De nombreuses caractéristiques sont identiques à celles que Baker suggère comme étant propre aux adventices, comme par exemple le taux de croissance élevée, une large tolérance environnementale ou la production prolifique de petites graines (Tableau 1, Tableau 2). **La région méditerranéenne étant une région particulièrement sensible au changement climatique (Tuel and Eltahir, 2020) et caractérisée par une diminution des précipitations, nous posons l'hypothèse que les communautés adventices actuelles des vignobles méditerranéens sont plus stress-tolérantes que les communautés plus anciennes.**

*Tableau 2 Propriétés fonctionnelles des adventices et plantes invasives favorisées par le changement climatique selon Clements & Ditommaso (2011).*

<b>Propriétés fonctionnelles des adventices favorisées par le changement climatique selon Clements &amp; Ditommaso (2011)</b>	<b>Propriétés fonctionnelles qui caractérisent ce qu'est une adventice selon Baker (1965) (voir Tableau 1)</b>
Taux de croissance élevé (favorisé par l'augmentation des degrés jours)	Caractéristique 3 de Baker
Large tolérance climatique ou environnementale (capacité à s'adapter à de nouvelles conditions)	Associée à la caractéristique 8 de Baker
Temps de génération court	Associé à la caractéristique 4 de Baker
Production de nombreuses petites graines	Caractéristique 8 de Baker
Très bonne capacité à disperser	Caractéristique 10 de Baker
Autogamie	Caractéristique 6 de Baker
Absence d'exigences particulières de germination	Caractéristique 2 de Baker
Compétitivité élevée	Caractéristique 14 de Baker
Défense efficace contre divers ennemis naturels	Absence de la liste de Baker

### 3.2.3.2. *Les changements temporels de pratiques de gestion des adventices*

De l'époque romaine à la moitié du XIX<sup>ème</sup> siècle, les pratiques de gestion des adventices ont peu évolué (Maillet, 1992). A l'automne, les ceps de vignes sont « chaussés », c'est-à-dire qu'une bande de terre est retournée à la base des pieds avec une charrue pour protéger le vignoble du gel pendant l'hiver (Figure 9). A la fin de l'hiver, les ceps sont déchaussés et cette pratique permet de détruire les adventices présentes sur le rang (travaux illustrés dans la Figure 9). A floraison, l'inter-rang est travaillé superficiellement ainsi qu'en juillet et plus facultativement en août. Dans les années 70, les premiers herbicides sont autorisés en vigne (Chauvel et al., 2012) et sont appliqués sous le rang de vigne ou « en plein », c'est-à-dire sous le rang de vigne et sur l'inter-rang (Maillet, 1992). Le désherbage chimique se base sur l'utilisation conjointe d'herbicides de pré et de post-levée. Le désherbage, en plein adopté à l'origine dans les vignobles champenois et bourguignons, s'étend largement dans les régions viticoles du sud jusqu'aux années 2000s (Monteiro and Moreira, 2004). La prise de conscience des effets non intentionnels des pesticides dans les années 2000 marque un tournant dans les pratiques de gestion (Boyer, 2001; Chantelot, 2002; Groupe COLUMA Vigne de l'AFPP, 2001). Une plus grande combinaison de pratiques de gestion est utilisée, avec notamment l'adoption de la tonte et le réemploi du travail du sol. **Nous posons l'hypothèse que l'extensivité croissante de gestion des adventices (diminution des doses d'herbicides et adoption de stratégies mixtes) a favorisé des stratégies moins rudérales que les pratiques d'il y a 40 ans.**

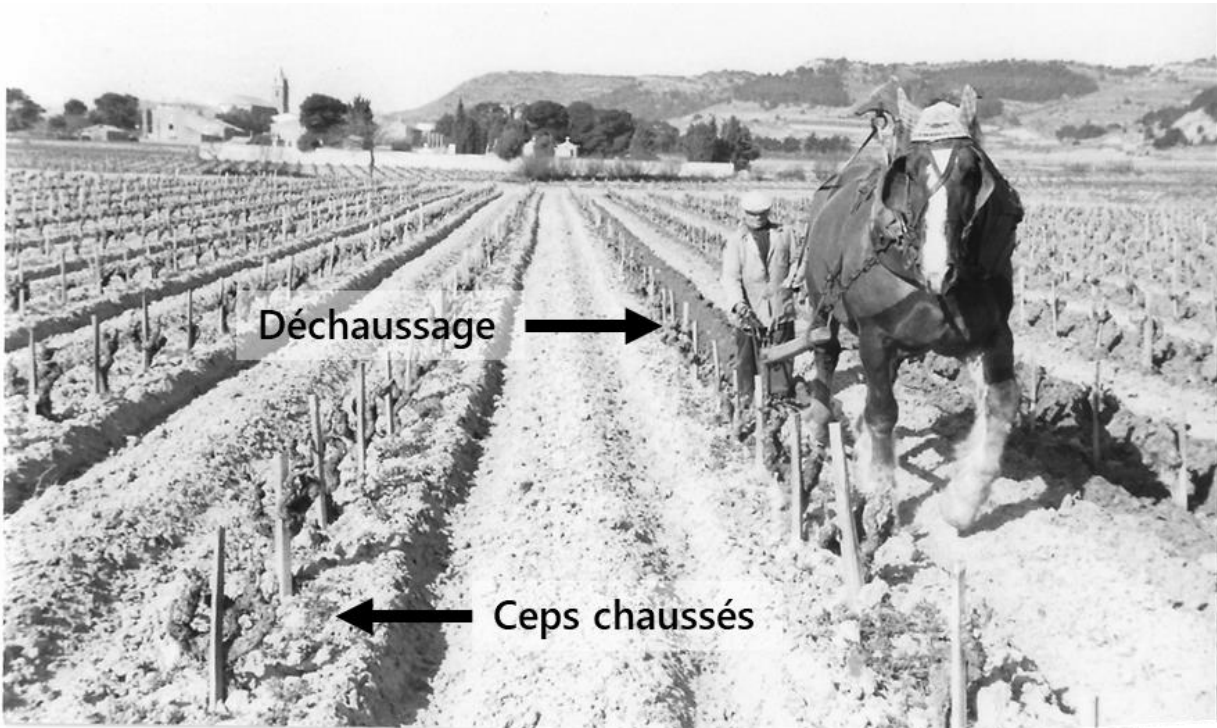


Figure 9 Déchaussage (aussi appelé décavaillonnage) des ceps de vigne au printemps. Photo prise par Régis Aymé en 1964, dans l'Aude.

### 3.3. Les métriques fonctionnelles à l'échelle des communautés

Pour évaluer la réponse fonctionnelle des communautés adventices aux pratiques de gestion des couvert, des métriques fonctionnelles à l'échelle des communautés sont nécessaires (Box 4) (Enquist et al., 2015). Dans cette thèse, **nous utilisons la moyenne pondérée par les abondances des espèces** (Community Weighted Means en anglais; CWM) (Garnier et al., 2004) **et des indices de diversité fonctionnelle** comme la variance par rapport à la moyenne pondérée (Community Weighted Variance, CWV) (Sonnier et al., 2010) ou l'indice d'entropie quadratique de Rao (Rao's Q) (Botta-Dukát, 2005) (Figure 10). Dans les études qui visent à démontrer le rôle des communautés de plantes sur le fonctionnement des écosystèmes, l'utilisation de ces métriques supposent deux grandes hypothèses: l'hypothèse « *Mass ratio* » (Grime, 1998) et l'hypothèse de complémentarité de niches (Petchey and Gaston, 2006). L'hypothèse *Mass ratio* (métrique fonctionnelle: CWM) postule

que les valeurs de traits des espèces affectent les processus des écosystèmes proportionnellement à leurs biomasses (Garnier et al., 2004; Grime, 1998). L'hypothèse de complémentarité de niche (métrique fonctionnelle: indice de diversité fonctionnelle) stipule que la dissimilarité entre espèces en termes de valeurs de traits maximise la diversité de stratégies d'utilisation des ressources (Petchey and Gaston, 2006; Sonnier et al., 2010). L'utilisation conjointe de ces deux moments fonctionnels permet de tester ces deux hypothèses d'effet des communautés végétales sur le fonctionnement des écosystèmes. Dans le contexte des vignobles, Kazakou et al. (2016) fait l'hypothèse que la diversité fonctionnelle des communautés adventices issues de parcelles à enherbement permanent, géré par des tontes est plus élevée que les celles des communautés adventices issues de parcelles travaillées. **Dans la thèse, nous faisons la même hypothèse en ajoutant l'hypothèse que le désherbage chimique, à l'image du travail du sol, est également associé à une diversité fonctionnelle faible.**

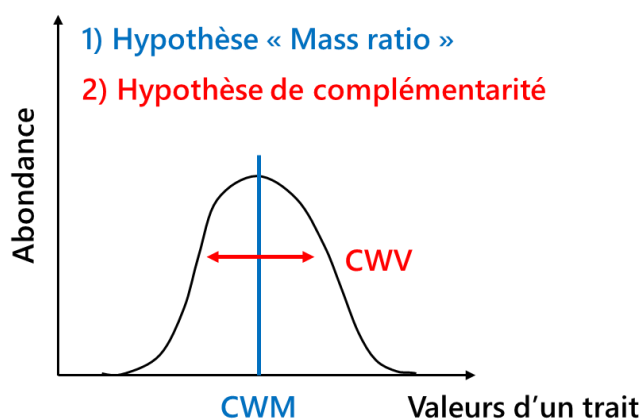
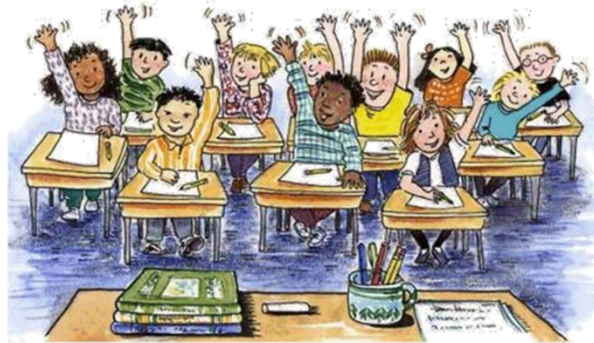


Figure 10 Les deux moments de la distribution des valeurs de traits à l'échelle des communautés, employés dans la thèse. Premièrement, l'utilisation de la moyenne pondérée par l'abondance des espèces (CWM, Community Weighted Mean) pour expliquer le fonctionnement des écosystèmes suppose que les espèces les plus abondantes au sein d'une communauté sont celles qui sont le plus impliquées dans son fonctionnement (Garnier et al., 2004). Deuxièmement, l'utilisation d'indices de diversité fonctionnelle comme ici la variance fonctionnelle d'une communauté (CWV, Community Weighed Variance) suppose que la dissimilarité entre espèces en termes de valeurs de traits maximise la diversité de stratégies d'utilisation des ressources (Sonnier et al., 2010).



**Box 4 Caractérisation d'une classe d'élèves par analogie à une communauté adventice en utilisant l'approche taxonomique et fonctionnelle.**

Si l'on prend l'exemple d'une classe d'élèves, analogues à une communauté d'adventices, l'approche taxonomique consiste à lister les noms de chaque élève et de noter s'ils et elles sont présent·e·s ou absent·e·s. Complémentairement, l'approche fonctionnelle quantifie une série de traits caractérisant les élèves, les moyenne à l'échelle de la classe et y associe une variance: la taille, le poids ou encore si certain·e·s élèves ont une aptitude à végéter l'après-midi...



**APPROCHE TAXONOMIQUE**

Prénom	Présence/absence
Camille	Présent·e
Paul	Absent·e
Charlie	Présent·e
...	
Nombre d'élèves	11

**APPROCHE FONCTIONNELLE**

Trait	Valeur moyenne	Variance
Hauteur	1m30	26 cm
Poids	45 kg	11 kg
Végète l'après-midi	Oui : 3	2
	Non : 8	4

## **4. Quelle contribution des communautés adventices au processus de recyclage de la matière organique dans les agroécosystèmes viticoles ?**

### **4.1. La multifonctionnalité encore sous explorée des communautés adventices des vignobles**

La compétition des adventices avec la vigne pour les ressources azotées et hydriques peut conduire à une baisse significative du rendement viticole. Par exemple, dans le cas d'une parcelle viticole uniquement tondue en Espagne, 42% de perte de rendement a été quantifiée en comparaison avec une vigne gérée par une combinaison d'herbicides et de travail du sol (Guerra et al., 2022). En Turquie, 13 % de perte de rendement a été estimé entre vignes travaillées et vignes enherbées naturellement et 29% entre vignes désherbées et vignes enherbées naturellement (Firat, 2020). Certaines études ont également démontré que la présence d'adventices n'était pas associée à une perte de rendement significative mais à une diminution d'azote dans les moûts (Kazakou et al., 2016; Smith et al., 2009).

Les communautés adventices contribuent également au fonctionnement des agroécosystèmes (Gaba et al., 2014): elles améliorent de la qualité du sol (Garcia et al., 2020), sont sources de nourriture pour les pollinisateurs (Gaba et al., 2017), pour les granivores comme les vers de terre, fourmis, carabes, oiseaux, rongeurs (Franke et al., 2009) et constituent une ressource fourragère de qualité (Genty et al., 2022). Les vignobles méditerranéens sont particulièrement sensibles aux risques d'érosion et à la perte de matière organique, notamment dus à l'intensité des pluies, le faible apport d'amendement, l'espacement entre les inter-rangs et l'intensité des pratiques de gestion des sols (Garcia et al., 2018; Novara et al., 2018; Romero et al., 2022). La gestion de la biomasse adventice étant un levier important de l'amélioration de la qualité des sols des systèmes viticoles (Garcia et al., 2018), **la thèse est centrée sur l'effet des communautés adventices sur le**

recyclage de la matière organique lorsqu'elles sont restituées au sol et sur deux processus principaux: la décomposition de la biomasse adventice et le recyclage minéral de l'azote, notamment les étapes de nitrification et dénitrification.

## 4.2. La décomposition de la biomasse végétale des communautés adventices

A notre connaissance, la décomposition de la biomasse végétale des communautés adventices après destruction et restitution au sol n'a pas été quantifiée dans la littérature (Figure 13). Pourtant, la décomposition de la biomasse végétale est l'un des processus majeurs impliqués dans le recyclage des nutriments et du carbone (Buchholz et al., 2017; Pingel et al., 2019) et un levier pour limiter la perte de qualité des sols des agroécosystèmes viticoles. La décomposition est définie comme la dégradation physique et chimique de la matière organique par l'action des organismes et des facteurs abiotiques, aboutissant à la libération des éléments minéraux dans une forme disponible pour les plantes (Begon, 2005). Trois processus se succèdent dans le temps (Figure 11) (Barantal, 2011; Chapin et al., 2012): (i) le lessivage des constituants solubles de la plante, (ii) la fragmentation de la biomasse par la macrofaune, et (iii) l'altération chimique par les microorganismes.

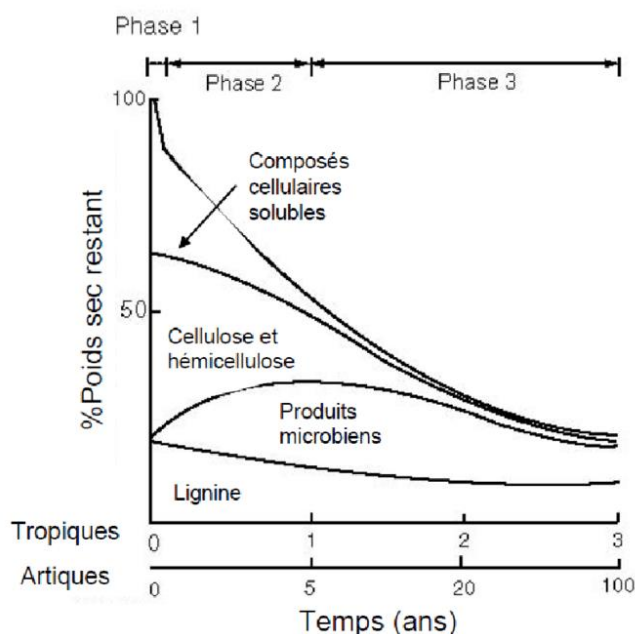


Figure 11 Les trois phases successives de la décomposition de la biomasse végétale: (i) lessivage des composés cellulaires solubles, (ii) fragmentation de la biomasse par la macrofaune et (iii) altération chimique de la biomasse en décomposition par les microorganismes. Figure issue de la thèse de Sandra Barental (2011).

En écologie, de nombreux travaux ont quantifié la décomposition de la litière, soit l'ensemble des feuilles mortes et débris végétaux, naturellement présente dans les systèmes naturels et semi-naturels. Par exemple, la teneur en matière sèche des feuilles, qui renseigne l'investissement des espèces dans des feuilles résistantes et à longue durée de vie, influence négativement la décomposition de la litière à l'échelle spécifique (Kazakou et al., 2009) et à l'échelle des communautés (Fortunel et al., 2009). Il a été démontré que les espèces à stratégie de conservation de ressources (teneur en fibres élevée, ratio entre la teneur en carbone et la teneur en azote élevée, ratio entre la teneur en lignine et la teneur en azote élevé) sont plus faiblement décomposables (de la Riva et al., 2019) (Figure 12). Dans les agroécosystèmes, les adventices sont souvent détruites avant qu'elles ne constituent de la litière. A notre connaissance, il n'existe pas d'études sur la décomposition potentielle de la biomasse que constitue les adventices des vignobles lorsqu'elles sont détruites et sur l'influence des pratiques de gestion sur la décomposition potentielle via leurs effets sur les communautés adventices. **Dans cette thèse, nous posons l'hypothèse que les communautés adventices désherbées chimiquement et travaillées ont des stratégies d'acquisition de ressources et sont plus décomposables que les communautés issues de parcelles viticoles tondues.**

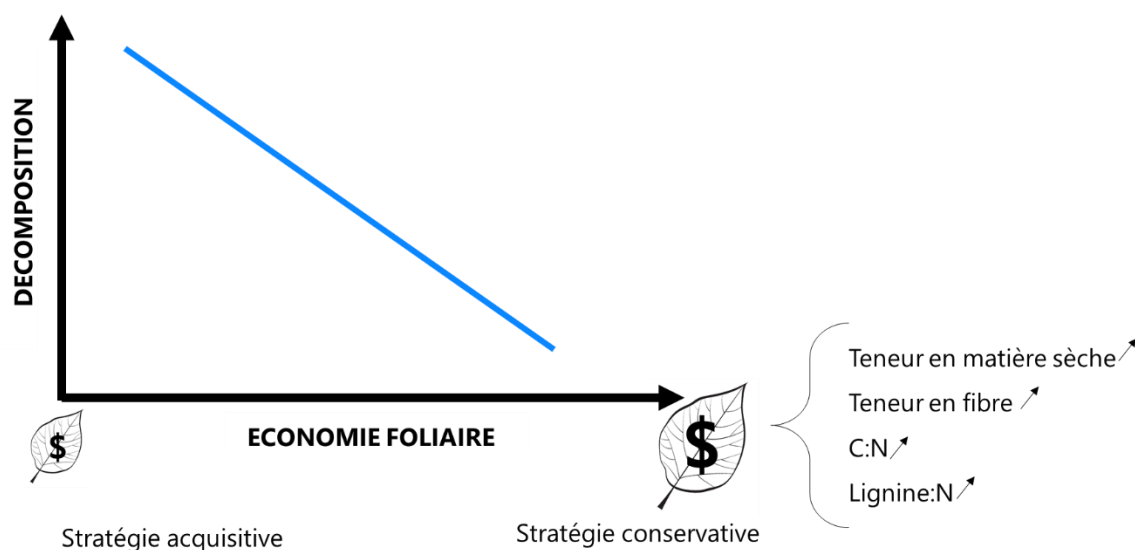


Figure 12 Relation entre le taux de décomposition des litières et les stratégies foliaires des espèces selon De La Riva et al. (2019).

### 4.3. L'influence des communautés adventices sur les processus microbiens du recyclage de l'azote

A la suite de la décomposition de la biomasse adventice, deux processus majeurs déterminent la disponibilité en azote dans les écosystèmes: la nitrification et la dénitrification (Figure 13). La nitrification est un processus aérobique en deux étapes effectué par des microorganismes autotrophes (Robertson, 1982). Ce processus est déterminé par la concentration en ammonium dans le sol (substrat de la réaction) et la teneur en eau du sol (Koskinen and Keeney, 1982; Zumft and Körner, 1997). La dénitrification est un processus anaérobique qui réduit les nitrates et les nitrites en formes gazeuses d'azote par des microorganismes hétérotrophes (Skiba, 2008). La dénitrification est déterminée par la concentration de nitrates dans le sol (substrat), le pH, la matière organique et la teneur en eau du sol (Skiba, 2008).

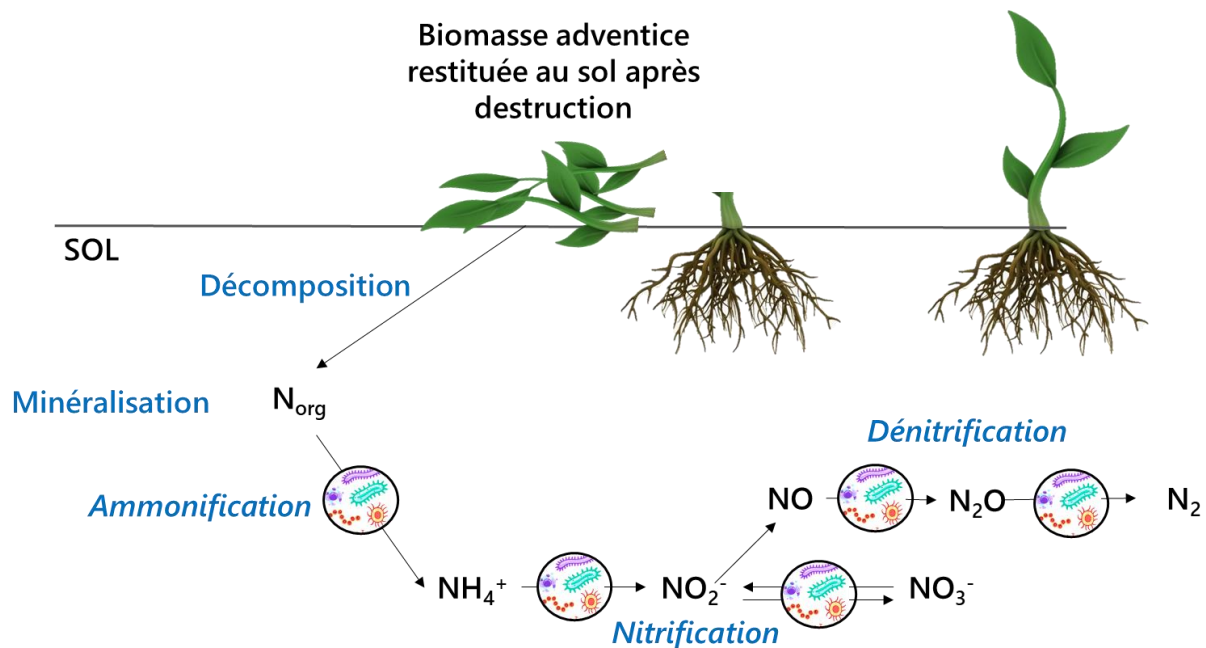


Figure 13 Le cycle de l'azote : de la décomposition de la biomasse adventice à la dénitrification.

Les communautés adventices peuvent influencer les communautés microbiennes nitrifiantes et dénitrifiantes *via* divers mécanismes dont l'absorption des substrats des deux processus (ammonium ou nitrate) (Cantarel et al., 2015; Grigulis et al., 2013; Laughlin, 2011), la régulation de la teneur en eau du sol (Abalos et al., 2019) ou *via* l'exsudation de composés carbonés par les racines, nécessaires aux microorganismes hétérotrophes (Moreau et al., 2019). Peu d'études ont exploré les liens entre les processus du cycle de l'azote et les propriétés fonctionnelles des communautés végétales, et, à notre connaissance, aucune n'a été faite en milieu agricole. Les plantes à stratégie acquisitive ont été associées à des potentiels de nitrification élevés (Cantarel et al., 2015; Laughlin, 2011; Orwin et al., 2010) dus à un cycle de l'azote plus rapide (décomposition de la biomasse et minéralisation plus rapide) et une immobilisation réduite de l'azote au sein de la biomasse microbienne (Henneron et al., 2020). Les relations entre les traits et le potentiel de dénitrification sont moins cohérentes entre les études. Certaines études ont démontré que les espèces conservatrices avaient un impact négatif sur le potentiel de dénitrification (Abalos et al. 2019) mais quelques études ont également démontré l'existence d'effets positifs (Cantarel et al., 2015; Legay et al., 2020). **Nous posons l'hypothèse que les communautés adventices désherbées chimiquement et travaillées à stratégies d'acquisition de ressources sont associées à un recyclage de l'azote plus rapide et à des abondances plus élevées de microorganismes nitrifiants et dénitrifiants.**

## **5. Le cadre conceptuel « Réponse-Effet » appliqué aux communautés adventices des vignobles**

Dans cette thèse, nous avons utilisé un cadre conceptuel permettant de relier les effets des pratiques de gestion des adventices à leurs fonctionnalités au sein des agroécosystèmes viticoles. Ce cadre conceptuel nommé « *Réponse-Effet* », établi dans un premier temps pour les écosystèmes naturels et semi-naturels, permet de prédire simultanément l'influence des changements environnementaux (*e.g.* changement climatique) sur les communautés végétales et les changements associés sur le fonctionnement des écosystèmes (Lavorel and Garnier, 2002) (Figure 14). L'une des hypothèses centrales, est que les traits des communautés végétales permettent à la fois d'expliquer les réponses

des communautés aux filtres anthropiques et biotiques et leurs effets sur les écosystèmes. Le cadre distingue deux types de traits: (i) les traits de réponse, qui sont ceux qui sont affectés par les facteurs environnementaux et (ii) les traits d'effet qui déterminent l'influence des communautés végétales sur les processus de l'écosystème (Lavorel and Garnier, 2002). En 2018, Damour et al. adaptent ce cadre au contexte agricole. Le cadre est constitué d'un « module biophysique », qui décrit le fonctionnement biophysique de l'agroécosystème sur une base de traits de réponse et d'effet et un « module de décision », décrivant les choix des agricultrices et agriculteurs et leurs interactions sur le module biophysique. **Dans cette thèse, nous appliquons ce cadre conceptuel aux communautés adventices dans les vignobles, répondant aux pratiques de gestion et aux conditions pédoclimatiques d'une part et affectant les processus reliés au recyclage de la matière organique (décomposition, nitrification et dénitrification) d'autre part (Figure 15).**

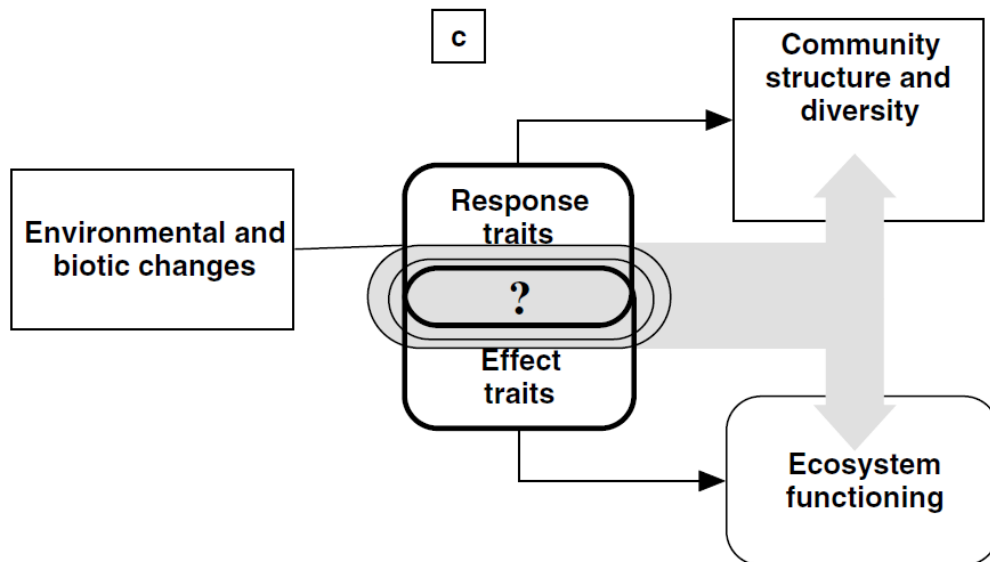


Figure 14 Le cadre conceptuel « Response-Effect » développé par Lavorel & Garnier (2002). Ce cadre permet de prédire simultanément l'impact des changements environnementaux (e.g. changement climatique) sur les communautés végétales et les changements associés sur le fonctionnement des écosystèmes.

## 6. Questions de recherche de la thèse

Très récemment, quelques études ont initié l'exploration de la réponse fonctionnelle des communautés adventices aux pratiques de gestion dans les vignobles (par exemple, celle de Hall et al. (2020)). **Les chapitres de thèse s'inscrivent dans la continuité de ces études, en explorant cette question à différentes échelles spatiales et dans le temps** (chapitres 1, 2, 3). Très peu d'études ont quantifié les liens entre les propriétés fonctionnelles des communautés adventices et le fonctionnement du sol dans les vignobles (à notre connaissance, il n'en existe qu'une parue à ce jour: (Garcia et al., 2020)). Ainsi, **la thèse comporte deux questions principales (Figure 15):**

- (i) **Quels sont les effets des conditions pédoclimatiques et des pratiques de gestion sur la structure fonctionnelle des communautés adventices à différentes échelles spatiales (régionale et nationale) et dans le temps (des années 1980s à 2020s) ?**
- (ii) **Comment les communautés adventices influencent-elles le recyclage de la matière organique, plus précisément la décomposition et l'abondance des communautés microbiennes nitrifiants et dénitrifiants ?**



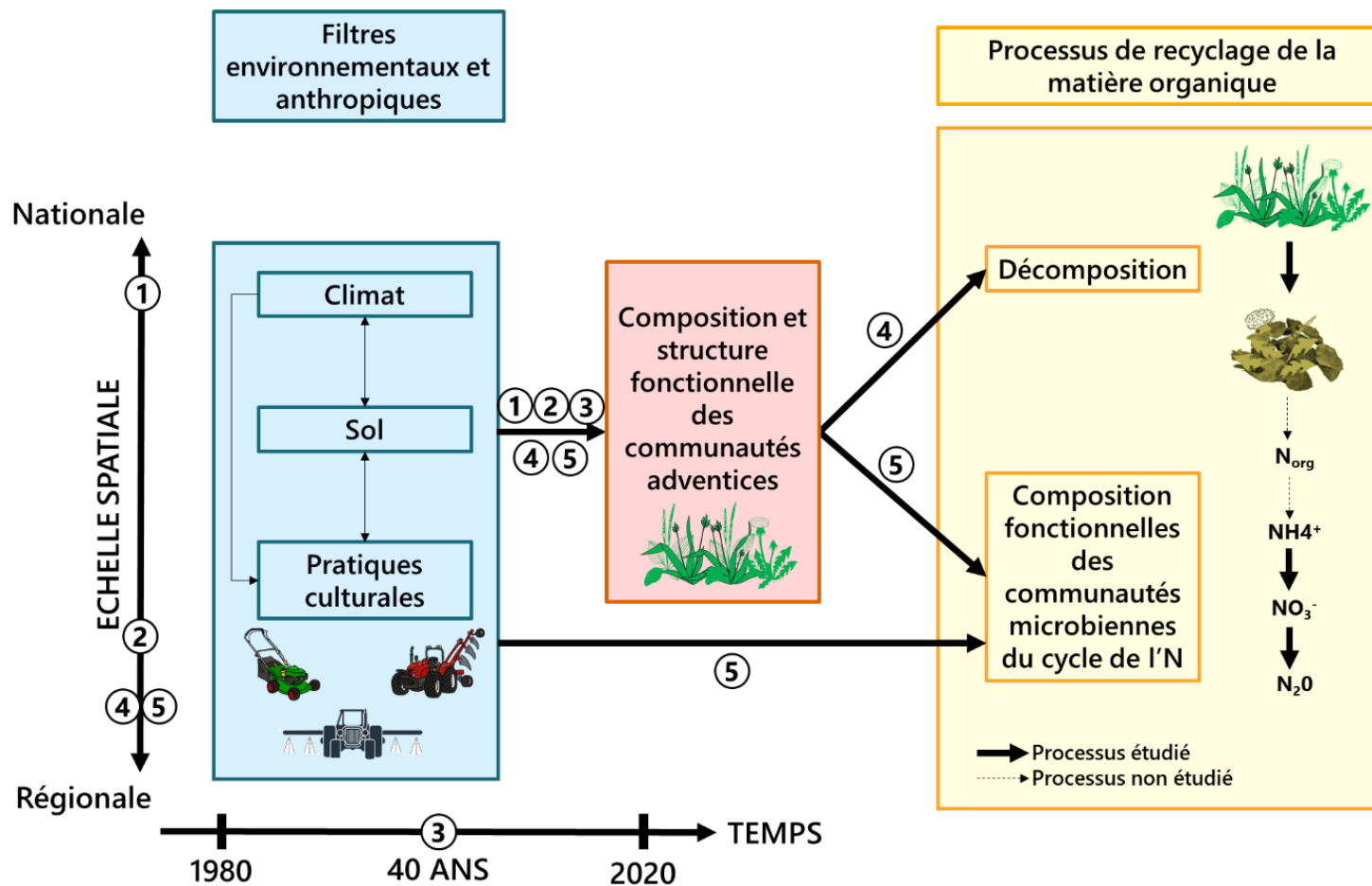


Figure 15 Schéma général de la thèse. Celle-ci s'articule autour de deux questions principales: (i) quels sont les impacts des conditions pédoclimatiques et des pratiques de gestion sur la structure fonctionnelle des communautés adventives et comment ces impacts modèlent les communautés à différentes échelles spatiales et temporelles (question traitée dans tous les chapitres de la thèse) et (ii) comment les communautés adventives influencent certains processus de recyclage de la matière organique, plus précisément la décomposition et l'abondance des microorganismes nitrifiants et dénitrifiants, en utilisant l'approche fonctionnelle (question traitée dans les chapitre 4 et 5). Le numéro des chapitres explorant les relations pratiques-traités (question 1 de la thèse) et traits-processus (question 2 de la thèse) sont indiqués. De plus, les échelles spatiales et temporelles considérées dans chaque chapitre sont annotées.

## 7. Démarches et structuration de la thèse

Pour répondre aux questions générales de la thèse, **trois réseaux de parcelles viticoles ont été mobilisés** (Figure 16). Un premier réseau nommé « Biovigilance Flore » est constitué de 45 parcelles de trois régions viticoles (Languedoc, Vallée du Rhône, Champagne) dont est issu le chapitre 1 de cette thèse (Figure 16). A l'échelle régionale du Montpelliérais, un second réseau de 40 parcelles a été mis en place dans le cadre de cette thèse, issu d'un réseau mobilisé par la thèse de Jacques Maillet en 1978 et 1979 (Figure 17). Les chapitres 3, 4 et 5 se basent sur ce réseau (Figure 16, Figure 17). Enfin, nous avons décidé d'intégrer les travaux explorant les effets des pratiques agricoles sur les communautés adventices, dans le Bordelais, bien que ces travaux ne fassent pas formellement partie de la thèse (chapitre 2). En effet, nous avons pensé que discuter les résultats de ce chapitre « hors thèse » permettrait d'étayer la discussion générale de la thèse.

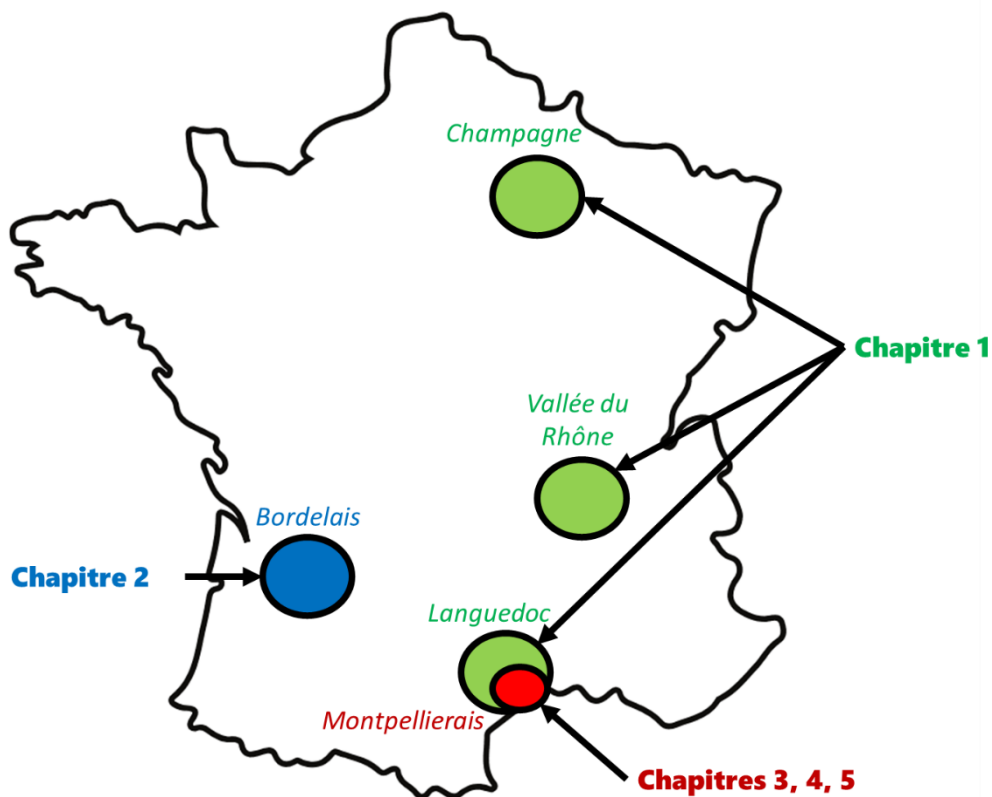


Figure 16 Localisation des réseaux de parcelles viticoles sur lesquelles se basent les résultats des différents chapitres de la thèse

**Les deux questions générales précédemment énoncées structurent la thèse en deux parties.** La première partie sur la réponse des communautés adventices aux filtres agro-environnementaux est traitée à différentes échelles spatiales (première sous-partie comprenant le chapitre 1 et 2) et dans le temps (deuxième sous-partie comprenant le chapitre 3). La deuxième partie interroge l'influence des communautés adventice sur les processus de recyclage de la matière organique avec deux chapitres: le chapitre 4, traitant de la décomposition potentielle des communautés adventices et le chapitre 5, traitant de l'abondance des communautés microbiennes nitrifiantes et dénitrifiantes dans les sols.

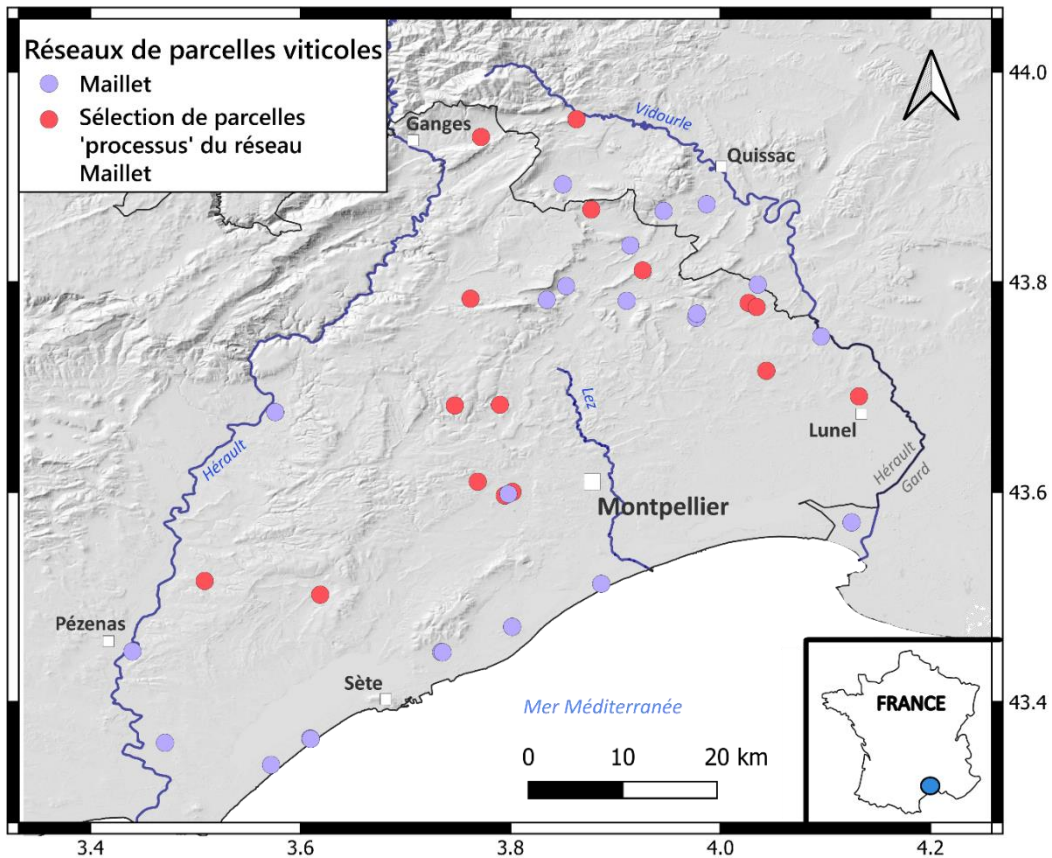


Figure 17 Réseaux de parcelles viticoles issus du réseau historique des années 1980s mis en place par Jacques Maillet. Le réseau 'Maillet' comprend 40 parcelles dont la flore a été observée en mars, juin et octobre 2020 et 2021 (points violet et rouge). Ce réseau a été mobilisé pour l'analyse temporelle des changements de communautés adventices entre les années 1980s et 2020s (chapitre 3). Le réseau 'Processus' comprend la sélection de parcelles viticoles au sein desquelles les traits des espèces adventices ont été mesurés ainsi que les indicateurs de processus de recyclage de la matière organique: décomposition, nitrification et dénitrification (chapitre 4 et 5).

## 8. Hypothèses générales de la thèse

Nous posons et testerons les hypothèses suivantes dans la thèse en réponse aux deux questions principales:

**(i) Hypothèses en réponse à la première question de la thèse: réponse fonctionnelle des communautés adventices aux conditions pédoclimatiques et agronomiques**

**a. Hypothèses d'importance relative des filtres pédoclimatiques et agricoles en fonction de l'échelle spatiale d'étude (chapitre 1, 2, 4 et 5)**

1. A l'échelle nationale, les conditions pédoclimatiques expliquent plus de variabilité fonctionnelle des communautés fonctionnelles que les pratiques de gestion du sol,
2. A l'échelle régionale, les pratiques de gestion du sol expliquent relativement plus de variabilité fonctionnelle par rapport aux conditions pédoclimatiques et par rapport à l'échelle nationale.

**b. Hypothèse de l'intensité de perturbation des pratiques de gestion (tous les chapitres)**

1. Le travail du sol et le désherbage chimique constituent des perturbations plus intenses car ces deux pratiques détruisent l'intégralité de la biomasse adventice,
2. La tonte constitue une perturbation moins intense que le travail du sol et le désherbage chimique car elle ne détruit qu'une partie de la biomasse adventice.

**c. Hypothèses de l'effet des pratiques de gestion sur les propriétés fonctionnelles des communautés adventices (chapitres 1 et 4)**

1. Les communautés adventices issues de parcelles viticoles désherbées et travaillées sont des communautés adaptées à des milieux très perturbés, rudérales et à stratégies d'acquisition de ressources,
2. Les communautés adventices issues de parcelles viticoles tondues sont des communautés moins perturbées, moins rudérales, plus compétitives et à stratégies de conservation de ressources.

**d. Hypothèses de l'effet des pratiques de gestion sur la diversité fonctionnelle des communautés adventices (tous les chapitres)**

1. Les communautés adventices issues de parcelles viticoles désherbées et travaillées sont des communautés à faible diversité fonctionnelle car le désherbage chimique et le travail constituent des perturbations intenses,
2. Les communautés adventices issues de parcelles viticoles tondues sont des communautés à diversité fonctionnelle élevée car la tonte constitue une perturbation moins intense que le travail du sol et le désherbage chimique.

**e. Hypothèses de l'effet des pratiques de gestion et du changement climatique sur les propriétés fonctionnelles des communautés adventices des années 1980s à 2020s (chapitre 3)**

1. Le climat a significativement changé entre les années 1980s à 2020-2021 et il favorise des communautés adventices stress-tolérantes,
2. Les pratiques de gestion des adventices sont devenues plus intégrées des années 1980s à 2020-2021 et ont sélectionné des communautés adventices moins rudérales.

**(ii) Hypothèses en réponse à la deuxième question de la thèse: l'effet des pratiques de gestion sur les propriétés fonctionnelles des communautés adventices et leurs relations avec les processus de recyclage de la matière organique (chapitre 4 et 5)**

1. Les communautés adventices issues de parcelles viticoles désherbées chimiquement et travaillées sont des communautés à stratégies d'acquisition de ressources favorisant un recyclage de la matière organique rapide (décomposition potentielle élevée, abondances de microorganismes nitrifiants, dénitrifiants et biomasse microbienne élevées),
2. Les communautés adventices issues de parcelles viticoles tondues sont des communautés à stratégies plus conservatrices que les communautés issues de parcelles désherbées chimiquement et travaillées, favorisant un recyclage de la matière organique plus lent (décomposition potentielle faible, abondances de microorganismes nitrifiants, dénitrifiants et biomasse microbienne faibles).



# **Partie 1 - Réponse des communautés adventices des vignobles aux pratiques de gestion du sol et au pédoclimat, à différentes échelles spatiales et dans le temps**



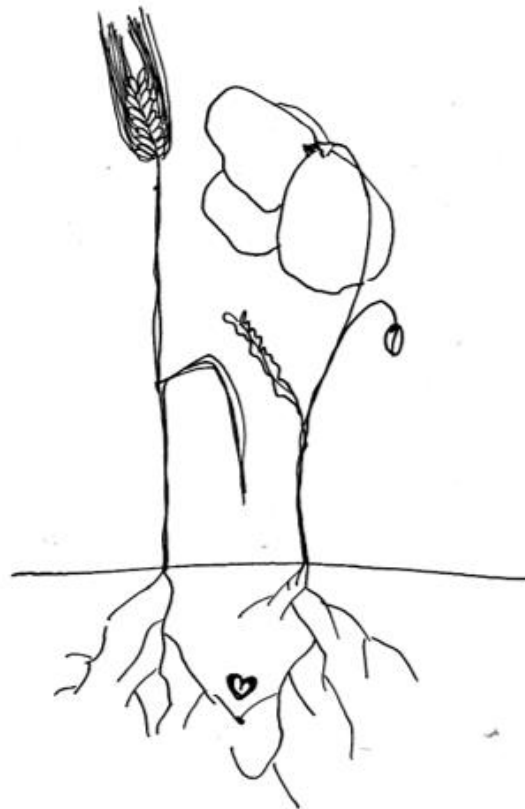
Travail du sol en traction animale

Photos de Régis Aymé (quelque part dans l'Aude, 1964)





# Sous-partie 1 - Réponse des communautés adventices des vignobles aux pratiques de gestion du sol et au pédoclimat, à différentes échelles spatiales



Dessin d'une adventice par une écologue anonyme

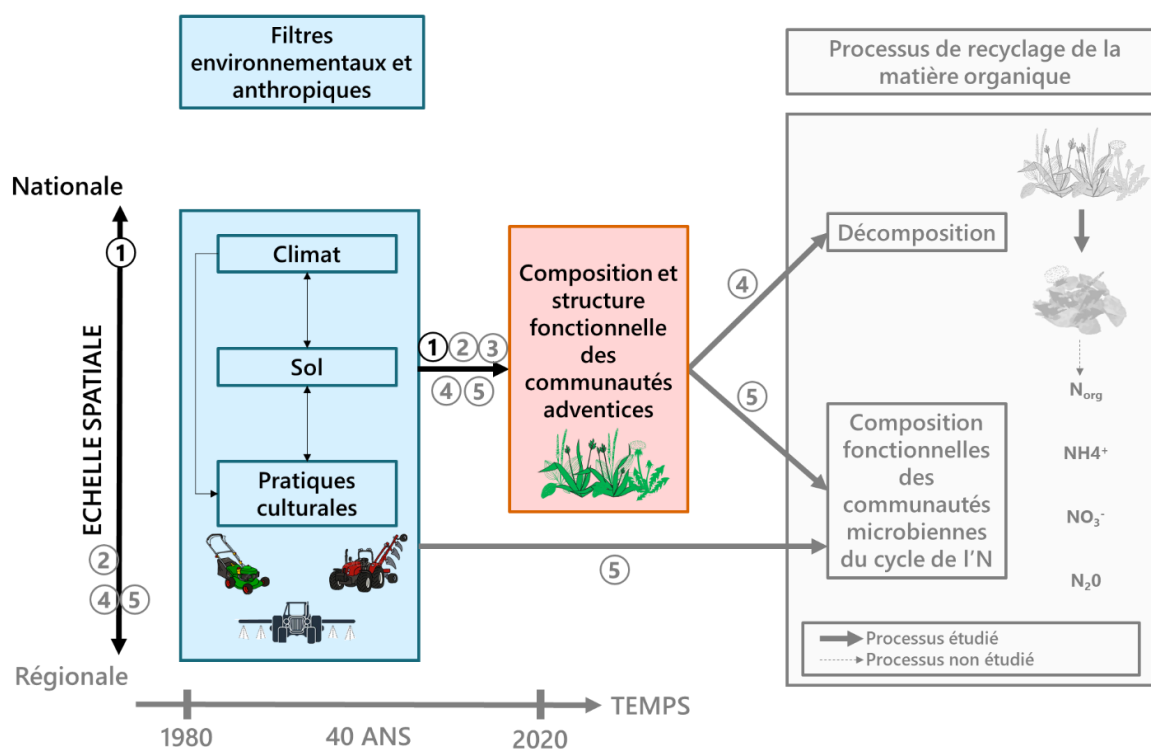


# Chapitre 1 - Relative importance of region, seasonality and weed management practice effects on the functional structure of weed communities in French vineyard

Bopp, M.-C., Kazakou, E., Metay, A., & Fried, G. (2022). Relative importance of region, seasonality and weed management practice effects on the functional structure of weed communities in French vineyards. *Agriculture, Ecosystems & Environment*, 330, 107892. <https://doi.org/10.1016/j.agee.2022.107892>

Ce chapitre a également été vulgarisé dans l'Union Girondine (Article de vulgarisation 2 en Annexe):

Bopp, M., Kazakou, E., Metay, A., Fried, G., 2022. Impact des pratiques de gestion des adventices sur la flore des vignes de trois grandes régions viticoles françaises. Union Girondine.





## **Présentation du chapitre**

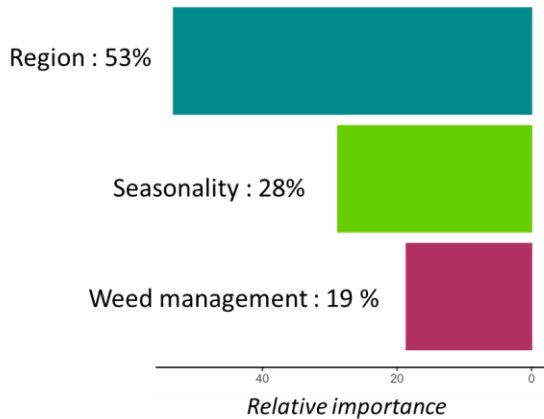
Ce chapitre est basé sur un jeu de données de relevés floristiques « *Biovigilance Flore* » de trois grandes régions viticoles françaises (Champagne, Languedoc et vallée du Rhône), observés de 2006 à 2012 (n= 270 relevés floristiques). Fried et al., (2019) ont quantifié l'influence relative des conditions pédoclimatiques et des pratiques de gestion des adventices sur la structure taxonomique des communautés. **L'objectif général de ce chapitre est de tester si les changements de composition en espèces causés par les filtres environnementaux et anthropiques démontrés dans Fried et al. (2019) entraînent également des changements dans la structure fonctionnelle des communautés adventices. Les hypothèses de cette étude sont les suivantes:**

- (i) Les conditions pédoclimatiques (rassemblées en effet 'Région') et la saisonnalité des relevés floristiques (sortie d'hiver, été, automne) expliquent plus de variabilité fonctionnelle que les pratiques,
- (ii) Les communautés adventices issues de parcelles viticoles désherbées et travaillées sont des communautés adaptées à des milieux très perturbés, rudérales et à stratégies d'acquisition de ressources,
- (iii) Les communautés adventices issues de parcelles viticoles tondues sont des communautés moins perturbées, plus compétitives et à stratégies de conservation de ressources.

Nous démontrons que la région viticole, la saisonnalité et les pratiques de gestion expliquent respectivement 53%, 28% et 19% de la variance fonctionnelle des communautés adventices (Figure 18). Les propriétés fonctionnelles des communautés fonctionnelles varient le long de deux gradients de pratiques: (i) un gradient de perturbation du sol des parcelles travaillées (perturbation mécanique du sol élevée) aux parcelles désherbées chimiquement (faible perturbation mécanique) et (ii) un gradient de couverture végétale des parcelles tondues (couverture élevée) aux parcelles travaillées et désherbées chimiquement (couverture plus faible). En Languedoc, le désherbage chimique favorise des communautés adventices rudérales (faible masse de graines, petite stature) tandis que les communautés issues de parcelles viticoles tondues sont plus compétitives (masse de graines plus élevée, hauteur maximale plus élevée et SLA plus faible). En Languedoc et en Champagne, le travail du sol favorise les communautés ayant une masse de graines élevée qui augmente la viabilité des

graines enterrées et des capacités de propagation latérale élevées, associées à la capacité de repousser après le travail du sol (e.g. espèces à rhizomes).

**1** Factors impacting functional structure of weed communities in vineyards



**2** Community response to weed management

E.g. in Languedoc :

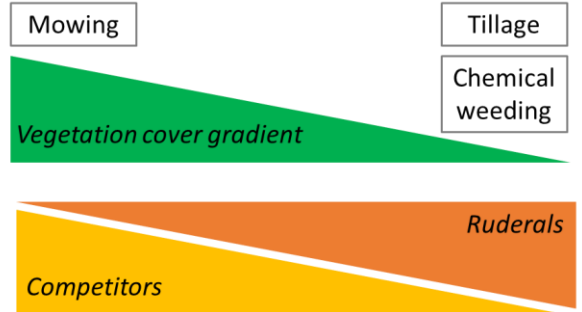


Figure 18 Résumé graphique du chapitre 1. (1) Le pédoclimat (variables rassemblées en l'effet région) est le premier facteur impactant les propriétés fonctionnelles des communautés adventices (53% de variance expliquée), suivi de la saisonnalité (28% de variance expliquée) et des pratiques de gestion des adventices (19%). (2) En Languedoc, les communautés issues de parcelles viticoles tondues ont des stratégies plus compétitives que les communautés issues de parcelles désherbées et travaillées avec une couverture de sol plus faible.



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## Relative importance of region, seasonality and weed management practice effects on the functional structure of weed communities in French vineyards

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## ARTICLE INFO

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 Seasonality  
 Tillage  
 Chemical weeding  
 Mowing

## ABSTRACT

Winegrowers have diversified their weed management practices over the last two decades changing the structure and the composition of weed communities. Complementary to taxonomic studies, trait-based approaches are promising ways for a better understanding of weed community responses to environmental and agronomic filters. In the present study, the impacts of climate, soil characteristics, seasons and weed management practices (chemical weeding, tillage and mowing) were assessed on weed communities from 46 plots in three French wine-growing regions (Champagne, Languedoc and Rhône valley). These agro-environmental gradients structuring weed communities according to their combinations of traits were highlighted using multivariate analysis (RLQ). The impacts of these filters on Community Weighted Means (CWM) and Community Weighted Variance (CWV) of weed communities were analysed using mixed and null modelling. Our results showed that spatio-temporal and weed management practice variables explained from 13% to 48% of the total variance of CWM (specific leaf area, maximum height, seed mass, flowering onset and duration and lateral spread). Region, seasonality and management practices explained 53%, 28% and 19% of CWM marginal variance, respectively. Weed management impacted CWM and CWV through two main gradients: (i) a soil disturbance gradient with high mechanical disturbance of soil in tilled plots and low mechanical disturbance in chemically weeded plots and (ii) a vegetation cover gradient with high vegetation abundance in mowed plots compared to barer soils in tilled and chemically weeded plots. In Languedoc, chemical weeding filtered weed communities with ruderal strategy trait values (low seed mass, small-stature) while mowed communities were more competitive (higher seed mass, higher stature and lower SLA). In Languedoc and Champagne, tillage favoured communities with high seed mass that increases the viability of buried seeds and high lateral spread values associated to the ability to resprout after tillage. This study demonstrated that trait-based approaches can be successfully applied to perennial cropping systems such as vineyards, in order to understand community assembly to better guide weed management practices.

## 1. Introduction

Weed communities have an important role in maintaining biodiversity in agroecosystems, potentially delivering multiple ecosystem services as long as their negative impact on crops are limited (Gaba et al., 2015; Paiola et al., 2020; Storkey and Westbury, 2007; Winter et al., 2018). Understanding how weed communities respond to abiotic, biotic and anthropogenic factors is essential to better guide weed management practices and thus to increase their ecosystem services (e.g. climate regulation through carbon stockage, nitrogen supply) and decrease their ecosystem disservices (e.g. competition for soil water

(Mahaut et al., 2020).

In vineyards, winegrowers have diversified their weed management practices over the last two decades (Fernández-Mena et al., 2021; Novara et al., 2018; Simonovici, 2019). Chemical weeding, especially in inter-rows, is less applied seeing a change in favour of superficial tillage and mowing. These alternative practices have impacted the structure of weed communities (Fried et al., 2019; Gago et al., 2007; Steenwerth et al., 2016). For instance, the combination of tillage and mowing of inter-rows has been significantly associated with higher richness and abundance unlike tillage or chemical weeding (Fried et al., 2019).

In addition to the taxonomic characterization of weed communities,

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trait-based approaches can be used to explain the response of weed communities to environmental filters and weed management practices (Kazakou et al., 2016). Traits are any morphological, physiological or phenological features that are measurable at the individual level, from the cell to the whole-organism level (Violle et al., 2007). As with other environmental drivers (e.g. climate, soil characteristics, seasonality), weed management practices filter weed species within communities according to their trait values, or ‘response trait’ (Damour et al., 2018; Kazakou et al., 2016; Lavorel and Garnier, 2002). Filtering processes can shape functional structure of weed communities in two major dimensions. Firstly, the mean trait value of communities reflects the major weed strategy to adapt to local conditions (e.g. early flowering onset to avoid disturbance). Secondly, the range of possible trait values expresses the dissimilarity of weed strategies within a community (e.g. a wide range of flowering onset within a community might increase the probability that some species flower in a disturbed environment). Reduced or wide range of possible trait values, driven by agro-environmental filters, lead respectively to convergent or divergent distributions (Bernard-Verdier et al., 2012; Perronne et al., 2017).

So far, trait-weed management practices relationships have been mostly explored in annual cropping systems (Alarcón Vllora et al., 2019; Armengot et al., 2016; Fried et al., 2012; Hernández Plaza et al., 2015; Smith, 2006; Storkey et al., 2010; Trichard et al., 2013) while few studies have investigated these relationships in perennial crop systems such as the grapevine (Fiera et al., 2020; Hall et al., 2020; MacLaren et al., 2019; Mainardis et al., 2020). In vineyards, tillage, chemical weeding and mowing are the most frequent weed management practices applied in France (Simonovici, 2019). Tillage and chemical weeding can be considered to be high disturbances as they destroy pre-existing living plant biomass (Gaba et al., 2014; Grime, 1979). Highly disturbed soils can result in convergent trait values distributions within the communities and favour trait values associated to ruderal weed communities (species with short stature, small seeds and high specific leaf area) (Grime, 2006; Kazakou et al., 2016). In contrast, mowing only partially destroys weed biomass. This intermediate disturbance (Grime, 2006), leads to a more divergent trait distribution (i.e. increased range of possible trait values) and to more competitive weed communities as vegetation cover is expected to be higher (species with large stature, high seed mass and high specific leaf area) (Kazakou et al., 2016; Mainardis et al., 2020).

Moreover, other abiotic filters such as climate, soil characteristics or seasonality can impact the functional structure of weed communities strongly (Keddy, 1992). Firstly, climate (e.g. temperature, precipitation) affects functional metrics at the community level (Alarcón Vllora et al., 2019; Hall et al., 2020). For instance, Alarcón Vllora et al. (2019) found that climatic inter-annual fluctuations drove the functional structure of weed communities more than management practices in cereal-legume rotation. Secondly, seasonality was one of the main factors explaining weed community composition in annual crop fields (Fried et al., 2008; Hallgren et al., 1999; Lososová et al., 2004). However, few studies have explored the relative importance of those abiotic filters compared to weed management practices on functional structure of weeds in vineyards. Indeed, most studies have been made at the experimental level (except (Hall et al., 2020)) in fixed abiotic conditions without considering the effect of pedoclimatic variations.

In vineyards, some recent trait-based studies have considered functional diversity using various metrics (e.g. richness, evenness, divergence, dispersion) (Fiera et al., 2020; Hall et al., 2020; Mainardis et al., 2020). However, to the best of our knowledge, none of these studies have tested the filtering effect of weed management practices on variations in trait values of weed communities by using null models. These randomization procedures make it possible to distinguish the effect of the specific richness from the effect of the functional richness (Mason et al., 2013) that can be mixed up. Indeed, functional diversity metrics (functional richness, functional divergence, functional evenness...) depend partly on the number of species occurring within a community

(i.e. the more species in a community, the higher the probability that they might have different trait values) (Mouchet et al., 2010). Null model approaches are largely used in community ecology to detect signatures of niche-based mechanisms (Perronne et al., 2017) and could be applied to managed weed communities in vineyards.

In this study, the relative importance of the filtering effects of wine-growing regions covering a wide range of climate and soil characteristics, seasonality and weed management practices on the functional structure of weed communities was assessed using Fried et al. (2019) large data set of 46 vineyards (the Biovigilance network) from three wine-growing French regions (Champagne, Languedoc and Rhône valley). The general objective of our study was to test whether changes in weed species composition in vineyards caused by environmental and anthropogenic filters shown in Fried et al. (2019) would also lead to changes in functional structure. First, we highlighted the main agro-environmental gradients structuring weed communities according to their combination of traits, using multivariate analysis (RLQ). Then, two different aspects of the functional structure of the weed communities were assessed using trait values from databases: Community Weighted Means (CWM) which is the mean value of traits of weed communities, and Community Weighted Variance (CWV) which is the variability of these trait values within the community. We used mixed linear models to test the effects of the explanatory variables on the CWM of weed communities. Secondly, we evaluated the seasonality and weed management practices effects on CWM within each wine-growing region. Thirdly, we tested if CWV were significantly impacted by weed management practices and seasonality using a null model approach to disentangle the effect of functional variance from the effect only due to species richness (Perronne et al., 2017). We expected that seasonality and region would explain more CWM variability than weed management practices. We hypothesized that tillage and chemical weeding would restrict the range of possible trait values within weed communities leading to a convergent distribution of trait values and favour more ruderal strategies (Kazakou et al., 2016). On the contrary, we hypothesized that mowing would increase functional diversity within communities (divergent distribution) and favour more competitive strategies. Moreover, we hypothesized that intraspecific variation was lower than interspecific variation (species robustness assumption) (Garnier et al., 2001; Kazakou et al., 2014).

## 2. Materials and methods

### 2.1. Climate, soil characteristics and weed management practices

Weed surveys were performed in 46 vineyards from 2006 to 2012 in three main wine production regions in France (the ‘Biovigilance network’): i) Champagne, northeast France (10 plots) ii) Beaujolais and the northern Rhône valley, central east of France (18 plots), and iii) Languedoc, central south of France (18 plots) (for more details on the timing of plots survey, see Table A.1). The climate of Champagne is continental with oceanic influences (Table A.2). The mean annual temperature of Champagne is 10.1 °C with 657 mm annual rainfall in the surveyed plots (Table A.2). The climate of Rhône valley is semi-continental with a mean annual temperature of 11.4 °C and 776 mm annual rainfall in the surveyed plots. The climate of Languedoc is Mediterranean with a mean annual temperature of 14.1 °C and 686 mm annual rainfall in the surveyed plots.

The soils of the Champagne vineyard plots are silty (45.7%) with a neutral pH (pH of 7.1) with low bulk density (fine earth) mean value (1387.3 kg/m<sup>3</sup>) (Table A.2). Rhône valley soils are characterized by the highest soil organic carbon content (19.7%) with a slightly acidic pH (6.7). Languedoc plots soils are alkaline (pH of 7.5), have a high bulk density (1528 kg/m<sup>3</sup>) and have 27% of clay. A PCA using all the soil-climate variables was performed (Fig. A.1) and showed that plots were well discriminated according to their regions of origin (based on Kruskal-Wallis tests comparing the distribution of plot coordinates on

PCA Axes 1 and 2, Fig. A.2). Because of this strong correlation between regions and pedoclimatic variables, we have chosen to keep only the "region" variable, assuming that this largely represents the soil-climate differences.

Three different weed management practices were applied on rows and inter-rows in these vineyards: chemical weeding, tillage and mowing. As mowing on rows was only exceptionally applied in our dataset (applied in two plots in Rhône, representing 7 floristic surveys), we decided not to consider this variable. At the global dataset scale, chemical weeding concerned one third of the inter-rows and 90% of the rows. Farmers of the vineyard network used pre-emergence and post-emergence herbicides. Active ingredients of post-emergence herbicide were mostly glyphosate. Pre-emergence herbicide was mostly constituted of oryzalin. Tillage was applied on one third of the inter-rows and 17% of rows. Tillage was mostly superficial (mean of 12 cm and ranging from 5 cm to more than 20 cm). Mowing concerned one third of inter-rows.

Weed management practices differed according to wine-growing regions. In Languedoc, tillage was more common (70% of inter-row practices and 27% of row practices) and more frequent (1.5 tillage of inter-rows and 0.9 cultivations of rows per year) than in the other regions (Table 1). In contrast, inter-rows of plots in Champagne and Rhône were mostly chemically weeded and mowed. Rows were mainly chemically weeded in Champagne (84% of rows, 1.7 chemical weeding per year) and Rhône (95% of rows, 2.7 chemical weeding per year). The timing of weed management was quite similar between regions. On average, chemical weeding and tillage management were applied earlier (April-May-June) than mowing (June-July) by farmers.

2.2. Floristic surveys

From 2006–2012, floristic surveys were performed in late winter to early spring (January to April), summer (May to July) and late summer to early autumn (August to October) (see Table A.1 for more details). Two temporal variables were considered in this study: the year of floristic survey and the number of days between the 1st January of the same year and the day of the floristic survey, which is considered as an indicator of the seasonality. In each vineyard plot, plant species were surveyed over an area of 2000 m<sup>2</sup> (in a rectangle 50 m long and 40 m wide). To estimate species abundance, we used five abundance classes developed in Barralis (1976): '1', less than 1 individual/m<sup>2</sup>; '2', 1–2 individuals/m<sup>2</sup>; '3', 3–20 individuals/m<sup>2</sup>; '4', 21–50 individuals/m<sup>2</sup>; '5', more than 50 individuals/m<sup>2</sup>. We transformed these scores into a quantitative scaling using the median of the range of each density class as followed: '1', 0.5 individual/m<sup>2</sup>; '2', 1.5 individuals/m<sup>2</sup>; '3', 11.5 individuals/m<sup>2</sup>; '4', 35.5 individuals/m<sup>2</sup>; '5', 75 individuals/m<sup>2</sup>. A list of species and distinct abundance scores were noted for rows and inter-rows. However, in this study, we focused on the plot-scale flora

resulting from the combination of row and inter-row practices (following MacLaren et al., 2019). Therefore, plant community composition was estimated from the whole 2000 m<sup>2</sup> surveyed including both the row and the inter-row (hereafter vineyard plot scale) taking the maximum abundance score for species occurring in both areas. In total, 270 surveys were recorded at the vineyard plot scale (46 in Champagne, 102 in Languedoc and 122 in Rhône, Table A.1).

2.3. Traits data

Six plant traits were selected to capture plant responses to environmental variations and weed management practices. Three traits of the Leaf-Height-Seed (LHS) strategy scheme were selected (Westoby, 1998): (a) specific leaf area (SLA) which is the light-catching area deployed per unit of previously photosynthesized dry mass, is related to the speed of resources acquisition (Wright et al., 2004), (b) maximum height which expresses the possible amount of growth in an undisturbed environment and which is related to light and nutrient acquisition (Westoby et al., 2002), (c) seed mass which represents the 'colonisation-competition' trade-off (Moles and Westoby, 2006) illustrating two strategies: 'producing a large number of small seeds, each with low establishment ability and high colonizing capacity' and 'producing fewer, larger seeds, each with a higher chance of successful establishment' (Westoby et al., 2002). Three other traits related to persistence and regeneration in disturbed habitats were selected: (d) flowering onset, (e) flowering duration and (f) lateral spread ability. Lateral spread is a qualitative trait which represents species abilities to develop horizontally (species with rhizomes or forming tussocks); it is rated as followed: '1', therophytes; '2', perennials with compact unbranched rhizomes or forming small tussocks (less than 100 mm in diameter); '3', perennials with rhizomatous system or tussocks reaching from 100 to 250 mm; '4', perennials reaching diameter of 251–1000 mm.

The trait values were extracted from different databases: the LEDA Traitbase for SLA (Kleyer et al., 2008), Flora Gallica for maximum height (Tison and De Foucault, 2014), the Seed Information Database (SID) for seed mass (Royal Botanic Gardens Kew, 2021), Baseflor for flowering onset and duration (Julve, 1998) and lateral spread from Hodgson et al. (1995) supplemented by expert opinion (G. Fried, pers. com.).

We calculated the community weighted means (CWM) (Garnier et al., 2004) and the Community Weighted Variances (CWV) (Sonnier et al., 2010) of each trait at the vineyard plot scale using the following equations:

$$CWM = \sum_{i=0}^n p_i \times trait_i \tag{1}$$

$$CWV = \sum_{i=0}^n p_i \times (trait_i - CWM)^2 \tag{2}$$

Where  $p_i$  is the proportion of abundance of the species  $i$  within a com-

Table 1

Characteristics of weed management practices of rows and inter-rows in Champagne, Languedoc and Rhône. Combination of different management practices can be applied on rows or inter-rows so total percentage per region are not equal to 100%. Abbr., abbreviations; % plots, proportion of plots; freq, the number of weeding per year; Jan., January; Feb., February; Mar., March; Apr., April; Aug., August; Sept., September; Oct., October; Nov., November.

Location	Weed management practices	Abbr.	Champagne			Languedoc			Rhône		
			% plots	Freq	Timing	% plots	Freq	Timing	% plots	Freq	Timing
Inter-rows	Chemical weeding	Chem. IR	48%	0.6 (0–3)	May (Mar.–Aug.)	26%	0.5 (0–3)	May (Mar.–Oct.)	45%	0.7 (0–3)	May (Mar.–Aug.)
	Mowing	Mow.IR	63%	1.7 (0–5)	June (Mar.–Sept.)	13%	0.3 (0–3)	June (Apr.–Aug.)	52%	1.8 (0–5)	July (Mar.–Sept.)
	Tillage	Till.IR	28%	0.5 (0–4)	June (Mar.–Sept.)	70%	1.5 (0–5)	June (Jan.–Nov.)	7%	0.4 (0–4)	May (Feb.–Sept.)
Rows	Chemical weeding	Chem.R	84%	1.7 (0–5)	May (Feb.–Aug.)	85%	1.3 (0–3)	April (Mar.–Oct.)	95%	2.3 (0–4)	May (Mar.–Oct.)
	Tillage	Till.R	17%	0.6 (0–5)	June (Mar.–Aug.)	27%	0.9 (0–4)	May (Feb.–Oct.)	9%	0.2 (0–2)	May (Mar.–Aug.)

munity,  $trait_i$  is the value of trait of the species  $i$  and  $n$  is the total number of species within the community. CWM as the weighted average trait values of the community, expresses the most probable trait value of an individual randomly picked up within a community (Garnier et al., 2004). CWV expresses the variability of the trait values around the average value within the community (Sonnier et al., 2010).

#### 2.4. Data analyses

##### 2.4.1. RLQ and fourth-corner analysis

To characterize the covariation of the functional structure of weed communities with management practices and spatio-temporal variables (i.e. region, seasonality and the year of floristic survey), we combined an RLQ analysis and a fourth-corner approach using Dray et al. (2014) framework. RLQ analysis investigates co-inertia between 3 types of data: i) region, year and season of floristic surveys (i.e. the number of days since the beginning of the year) and soil management variables (R table), ii) floristic composition (L table), iii) species trait attributes (Q table). Species density were square-root transformed. Firstly, correspondence analysis (CA) was applied to the table L. Then, we performed a Hill and Smith analysis on the R and Q tables using respectively the row and the column scores of the CA. Finally, the RLQ performed two co-inertia analyses on the R-L and L-Q tables. A Monte Carlo permutation ( $n = 999$ ) test was used to test the global significance of the relationship between the agro-environmental table R and the trait table Q. Based on the results of the RLQ analysis, a fourth-corner analysis was performed to test the significance of the relationship between traits and agro-environmental variables. At this step, we tested the associations between individual traits and environmental gradients obtained from RLQ scores, and between individual environmental variables and trait syndromes obtained from RLQ scores. We used a permutation model ( $n = 49,999$ ) to test the null hypothesis that species are distributed independently of their trait values and their preferences for agro-environmental conditions in the vineyard plots (Dray and Legendre, 2008). Adjusted p-values were used rather than p-values to limit the overall error rate of multiple testing. Multivariate analyses such as RLQ give a good idea of the main agro-environmental gradients. To further understand the effect of each agro-environmental variable on each trait, we analysed the variations in CWM and CWV.

##### 2.4.2. Mixed linear models of CWM

To evaluate the relative importance of region, temporal variables and weed management practices effects on CWM, we constructed mixed linear models for each CWM ('lmer' function of lme4 package (Bates et al., 2015)). We defined two random effects in each model: the vineyard plot identity and the year of floristic survey. Seed mass, lateral spread and flowering duration were logarithmised to validate hypotheses of linear models. Prior to model construction, the collinearity of explanatory variables was investigated using the variance inflation factor ( $VIF < 5$ ). Model selection was performed using a backward step selection procedure based on AIC (Burnham and Anderson, 2004). We calculated the explained variance of each covariate as the percentage of variance additionally explained when each variable was added one by one to the model. As region had a major effect on CWM, we investigated the weed management practice variables, the seasonality and the year of survey effects on CWM within each region.

##### 2.4.3. Covariations between CWM and weed management practices and temporal variable gradients

To characterize the gradient of weed management practices and temporal variation of floristic surveys, we performed a Principal Component Analysis (PCA). Then, we tested the correlations between CWM and the PCA scores of the sites on the first two axes representing gradients of management practices (Spearman's rank correlation). We corrected p-values from multivariate testing using Bonferroni corrections.

##### 2.4.4. Null modelling and covariations between effect sizes of CWV and weed management practices and temporal variable gradients

To test whether CWV values were randomly distributed along the weed management practices gradient, we first used a null model approach. We constructed a 'population-based fixed-zero per sites' null model to test the following null hypothesis: abundance is randomly distributed within plots with respect to trait values. We shuffled species x site matrix for the observed species, while keeping species x trait matrix unchanged, breaking the link between abundance and trait values (Bernard-Verdier et al., 2012; Perronne et al., 2017). Thus, the richness, the list of the observed species and the abundance distribution within a plot remained unchanged. This randomization type allows to disentangle the effects of environmental and agronomic drivers on functional diversity from effects simply related to the richness of communities. For each plot, we calculated an effect size (ES) that quantifies the probability for each weed community that the observed CWV is higher or lower than 999 CWV randomly generated by null models (Bernard-Verdier et al., 2012; Kelt et al., 1995) (Eq. (3)).

$$ES = \text{number}(\text{null} < \text{obs}) / 999 - 0.5 \quad (3)$$

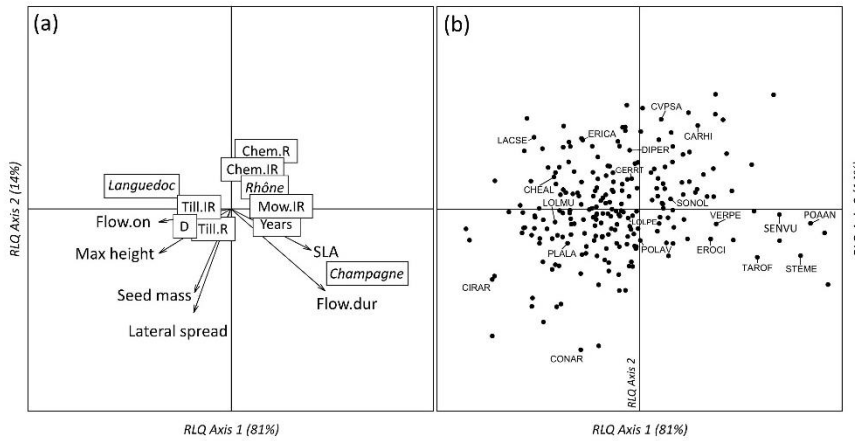
Where  $\text{number}(\text{null} < \text{obs})/999$ , is the proportion of simulated CWV generated by null models that are lower than the observed CWV for each community on 999 simulations. ES measures the strength of convergence and divergence (Botta-Dukát, 2018). ES values close to zero indicate that observed CWV values are not different from random CWV values. In contrast, high and low ES values quantify respectively strong divergent ( $0 < ES \leq 0.5$ ) and convergent ( $-0.5 \leq ES < 0$ ) functional structure of weed communities. In order to detect a general pattern of community structure regardless of the spatio-temporal and agronomic characteristics, we tested if ES was overall different from 0 using a two-tailed Wilcoxon signed-ranks test (Bernard-Verdier et al., 2012; Jung et al., 2010). To investigate the impact of the weed management practices gradient on CWV, we used the same procedure as for CWM. Within each wine-growing region, we tested the significance of correlations between effect sizes of CWV and the coordinates of the plots on the first two axes of the PCA, using Spearman's rank correlation. All the statistical analyses were performed with R (3.6.2 version). All multivariate analyses (RLQ, PCA) were conducted using ade4 package (Chessel et al., 2004).

### 3. Results

#### 3.1. Covariation of the functional structure of weed communities across management practices and spatio-temporal variables

The first two axes of the RLQ explained 95% of inertia (81% explained by the first axis and 14% explained by the second axis) (Fig. 1). The co-structure between R and Q was significant (Monte-Carlo test,  $P < 0.001$ ) demonstrating the global significance of the relationships between species traits and agro-environmental variables (region, seasonality, year of floristic survey and weed management practices as specified in Table 1). According to the fourth-corner analysis combined with the RLQ analysis, all the spatio-temporal and agronomic variables except Rhône region were correlated to the first axis of the RLQ, which described most of the variability (Fig. A.3a). The first RLQ axis opposed spring surveys to autumn surveys, earlier surveys to later surveys, chemically weeded rows and inter-rows to tilled rows and inter-rows, Champagne region to Languedoc region (Fig. 1a, A.3a).

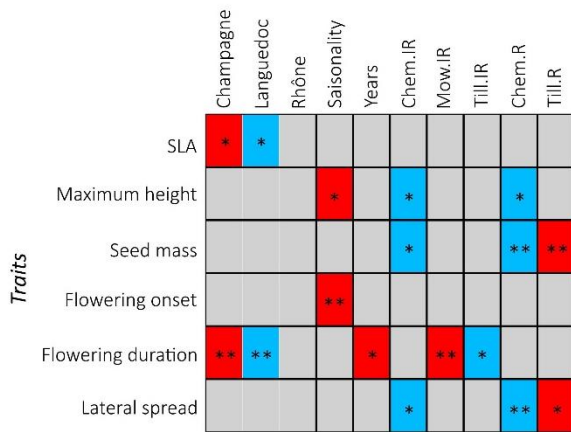
Weed species located in Champagne had high SLA and long flowering duration (e.g. *Stellaria media*) while those located in Languedoc had low SLA and short flowering duration (e.g. *Cirsium arvense*) (Figs. 1 and 2). Autumn species had larger stature and later flowering onset (e.g. *Cirsium arvense*) compared to spring species (e.g. *Crepis sancta*). Species identified during the last years of floristic surveys (e.g. 2011, 2012) had long flowering duration (e.g. *Taraxacum officinale*) (Figs. 1 and 2).



**Fig. 1.** RLQ results carried out on three matrices: R (270 floristic surveys x 10 agro-environmental variables), L (270 floristic surveys x 227 weed species) and Q (227 weed species x 6 traits). The agro-environmental variables and weed traits (a) and weed species (b) are displayed along the first two RLQ axes. Abbreviations used in (a) are: D, seasonality (number of days since the beginning of the year of floristic survey); Year, year of floristic survey; Flow.on, flowering onset; Max height, maximum height; Flow.dur, flowering duration; SLA, specific leaf area. The identities of the twenty most frequent species across all floristic surveys are specified in (b). CARHI, *Cardamine hirsuta*; CIRAR, *Cirsium arvense*; CONAR, *Convolvulus arvensis*; CHEAL, *Chenopodium album*; CVPSA, *Crepis sancta*; DIPER, *Diploxys erucoides*; ERICA, *Erigeron canadensis*; EROCI, *Erodium cicutarium*; GERRT, *Geranium rotundifolium*; LACSE, *Lactuca serriola*; LOLMU, *Lolium multiflorum*; LOLPE, *Lolium perenne*; PLALA, *Plantago lanceolata*; POAAN, *Poa annua*; POLAV, *Polygonum aviculare*; SENVU, *Senecio vulgaris*; SONOL, *Sonchus oleraceus*; STEME, *Stellaria media*; TAROF, *Taraxacum officinale*; VERPE, *Veronica persica*.

*Polygonum aviculare*; SENVU, *Senecio vulgaris*; SONOL, *Sonchus oleraceus*; STEME, *Stellaria media*; TAROF, *Taraxacum officinale*; VERPE, *Veronica persica*.

**Region, temporal variables and weed management practices**



**Fig. 2.** Significant associations of the fourth-corner tests between the agro-environmental variables and the species traits. Red boxes show positive correlations, blue boxes negative correlations and grey boxes non-significant relations. Years, year of floristic survey; SLA, specific leaf area. Significance of associations are referred as following: \*  $p < 0.05$ ; \*\*  $p < 0.01$ .  $p$  are adjusted  $p$ -values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Chemical weeding of rows and inter-rows were associated with low stature species, low seed mass and low lateral spread abilities (e.g. *Cardamine hirsuta*). Species in mowed plots had long flowering duration (e.g. *Veronica persica*) while species located in tilled inter-rows had short flowering duration (e.g. *Lolium multiflorum*) (Figs. 1 and 2). Species located in tilled rows had high seed mass and high lateral spread abilities (e.g. *Rubia peregrina*).

**3.2. Relative importance of the weed management practices and spatio-temporal variables explaining weed community's functional response**

Spatio-temporal and weed management practice variables explained from 13% to 48% of the total variance of CWM of the different traits

(Fig. 3, Supplementary 4). Overall, 'region' explained most of CWM marginal variance (53%), followed by seasonality (28%) and some weed management practice variables (19%).

The region of floristic surveys explained a large part of variance in maximum height (60%, Fig. 3a1), SLA (99%, Fig. 3b1), flowering onset (59%, Fig. 3e1) and duration of flowering (100%, Fig. 3f1). Weed communities from Champagne region had high SLA, early flowering onset and long flowering duration (Fig. 3b2, e2, f2 respectively). The estimate of flowering duration in Rhône was almost null (-0.02) but the effect was significant showing that duration of flowering was average in that region and different from Champagne's short duration of flowering and the long duration of flowering in Languedoc (Fig. 3f2).

'Seasonality' was the most frequently selected effect in CWM models. This explained significant proportions of variance of CWM of maximum height (35%, Fig. 3a1), seed mass (38%, Fig. 3c1), lateral spread (54%, Fig. 3d1), flowering onset (41%, Fig. 3e1) but low variance of SLA (<1%, Fig. 3b1). The communities of autumn floristic surveys had high stature (Fig. 3a2), high seed mass (Fig. 3c2), high lateral spread abilities (Fig. 3d2) late flowering onset (Fig. 3e2) and low SLA (Fig. 3b2).

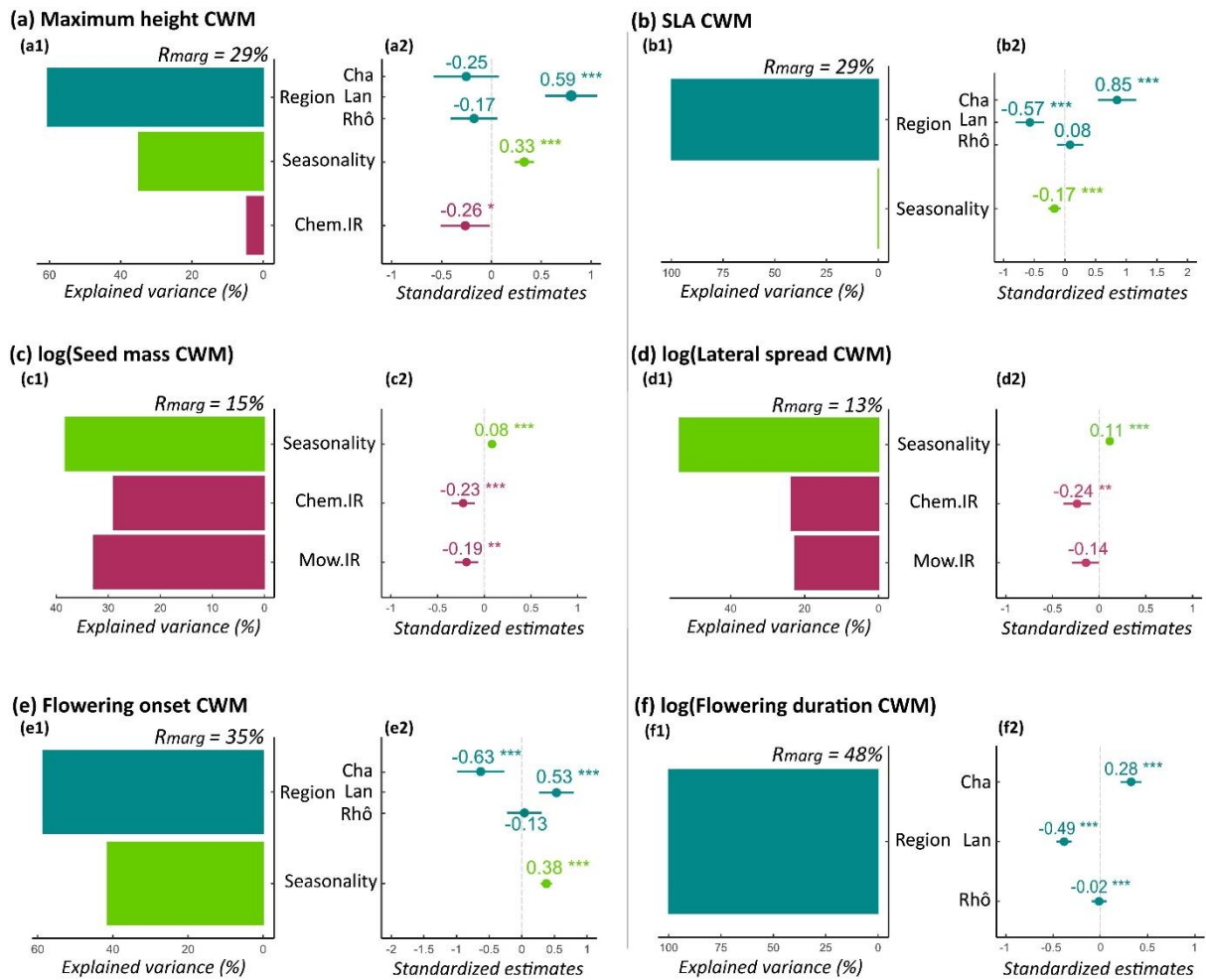
Chemical weeding and mowing explained large proportions of variance in seed mass (29% and 33% respectively, Fig. 3c1) and lateral spread (24% and 22% respectively, Fig. 3d1). Chemically weeded communities on inter-rows had low stature (Fig. 3a2), low seed mass (Fig. 3c2) and low lateral spread abilities (Fig. 3d2). Mowed weed communities in inter-rows showed low seed mass (Fig. 3c2) and low lateral spread tendency (Fig. 3d2). Tillage of rows and inter-rows had no direct effects on CWM of weed species and in general, the management of the rows did not impact significantly CWM of weed communities.

The plot random effect described significant proportions of total variance (35% of lateral spread abilities, 20% of seed mass, 13% of flowering duration, 10% of SLA, 9% of maximum height, 8% of flowering onset). The random effect of the year of the floristic survey was only selected in the flowering onset CWM model and represented 10% of the total variance of this CWM.

**3.3. Functional response of weed communities to weed management practices within each region**

**3.3.1. Community Weighted Means (CWM) response to weed management practices within each region**

In order to disentangle the effect of region from the effects of the other variables, we explored weed functional responses to weed



**Fig. 3.** Effects of region, seasonality and management practice variables on CWM of weed communities: (a) Maximum height CWM, (b) Specific Leaf Area (SLA) CWM, (c) logarithmised seed mass CWM, (d) logarithmised lateral spread CWM, (e) flowering onset CWM and (f) logarithmised flowering duration CWM. For each CWM, Figures (a1), (b1), (c1), (d1), (e1) and (f1) display the explained variance for each fixed effect selected in CWM models and the marginal variance (i.e. the total variance explained by all the fixed effect ( $R_{\text{marg}}$ )). Figures (a2), (b2), (c2), (d2), (e2) and (f2) report the standardized estimates of fixed effects selected in CWM models. Blue, green and red bars and texts represent respectively region, seasonality and weed management practices effects. Significance of estimated are referred as following: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ . CWM, Community Weighted Means. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

management practices, seasonality and year of survey within each region. Fig. A.4 displays the gradients of these variables, excluding the regional effect. The first two axes represented 54% of total variance. They described mostly weed management practices gradients (Table A.3). Seasonality and year of survey variables contributed poorly to total inertia of these axes (7% of explained variance for the first two axes). The first axis explaining 31% of variance opposed tilled rows and inter-rows (positive coordinates) and chemically weeded rows (negative coordinates). It represented the soil disturbance gradient from tilled soils with high below-ground mechanical disturbances to chemically weeded soils with low below-ground mechanical disturbance. The second axis explaining 23% of variance opposed mostly mowed inter-rows (negative coordinates) to combinations of tilled and chemical weeded inter-rows (positive coordinates). It represented the vegetation cover gradient with high vegetation cover in mowed inter-rows and low vegetation cover in tilled and chemically weeded inter-rows.

The significance and the values of the coefficients of correlation between CWM within each region and the first two axes of the PCA

performed on weed management practices, season and year of survey variables are reported in Table 2. The Fig. A.5–A.10 display CWM variation along these first two PCA axes. The effect of management practice on CWM differed according to the wine-growing regions (for means and standard deviations of CWM per region, see Table A.5).

In Languedoc, significantly higher CWM of seed mass and lateral spread abilities were found in tilled rows and inter-rows compared to chemically weeded rows (Table 2). Mowing was significantly associated with lower CWM for SLA and higher CWM for maximum height, seed mass, lateral spread abilities and flowering onset compared to chemically weeded inter-rows and to combined tillage and chemical weeding of inter-rows. In Champagne, tillage on rows and inter-rows was associated with higher lateral spread abilities as in the Languedoc region and higher maximum height compared to chemically weeded rows (Table 2). In the Rhône region, chemical weeding on rows was significantly associated with shorter flowering, higher stature and later flowering compared to tillage of rows and inter-rows (Table 2).

**Table 2**

Coefficients of correlation between Community Weighted Means (CWM) and weed management gradients (two first PCA axes, see Fig. A.4) for each region. P-values were corrected from multiple comparisons testing using Bonferroni correction. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ; no asterisks, non-significant ( $p > 0.05$ ). SLA, Specific Leaf Area; PCA, Principal Component Analysis.

CWM	Languedoc		Champagne		Rhône	
	1st PCA axis	2nd PCA axis	1st PCA axis	2nd PCA axis	1st PCA axis	2nd PCA axis
	Chem.R	Mow.IR	Chem.	Mow.	Chem.R	Mow.
	→ Till.	→	Chem.	Mow.	→ Till.IR,	Mow.
	IR, Till.R	Chem.IR + Till.IR	Till.IR,	Chem.	Till.IR	IR →
			Till.IR	IR + Till.IR		Chem.
						IR + Till.IR
Maximum height	0.06	-0.29**	0.41*	-0.2	-0.25*	-0.05
SLA	-0.12	0.31**	-0.17	0.26	0.09	0.06
Seed mass	0.26*	-0.4***	0.001	0.04	-0.01	-0.16
Lateral spread	0.53***	-0.32**	0.36*	-0.21	-0.09	-0.21
Flowering onset	0.01	-0.24*	0.07	-0.34	-0.33***	0.01
Flowering duration	0.05	0.16	-0.01	0.23	0.24*	-0.22

### 3.3.2. Community Weighted Variance (CWV) response to weed management practices within each region

Half of the CWV were significantly different from random expectations of null models (Fig. A.11–A.16). More precisely, most of the CWV were lower than expectations demonstrating a convergent distribution and a restricted variance of trait values within weed communities (for means and standard deviations of CWV per region, see Table A.5).

In the Champagne region, lateral spread CWV were convergent while flowering onset and duration had divergent distributions (Fig. A.14). In Languedoc, SLA, lateral spread, flowering onset and seed mass had convergent distributions (Fig. A.11 and A.12). In the Rhône, seed mass and lateral spread were convergent (Fig. A.15 and A.16). Four effect sizes out of 36 were significantly correlated to one axis of the PCA (Table 3) demonstrating different functional responses to the filtering effect of weed management practices. In Languedoc, the effect size of lateral spread CWV was positively correlated with the first axis, showing that species located in chemically weeded row communities had similar lateral spread abilities while species within tilled communities had dissimilar lateral spreading strategies (Table 3). In Champagne, the effect sizes of SLA CWV, flowering onset CWV and flowering duration CWV were positively correlated with the second axis (Table 3) demonstrating that combination of chemical weeding and tillage of inter-rows was associated with high variations of SLA, flowering onset and duration within weed communities.

## 4. Discussion

Our study highlighted that the functional structure of vineyard weed communities responded strongly to agro-environmental factors with high variation of trait values across regions, seasons and management practices. In addition to CMW, we explored the filtering effect of weed management practices through the analysis of CWV. To our knowledge, this is the first study to investigate weed management practice effects on the functional structure of weeds through null modelling of community weighted variances in vineyards. Null modelling has allowed us to test if CWV were restricted or increased by weed management, independently of the effect of weed management community richness shown in Fried

**Table 3**

Coefficients of correlation between effect sizes of Community Weighted Variance (CWV) and weed management gradients (two first PCA axes, see Fig. A.4) for each region. P-values were corrected from multiple comparisons testing using the Bonferroni correction. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ; no asterisks, non-significant ( $p > 0.05$ ). SLA, Specific Leaf Area; PCA, Principal Component Analysis.

Effect sizes of CWV	Languedoc		Champagne		Rhône	
	1st PCA axis	2nd PCA axis	1st PCA axis	2nd PCA axis	1st PCA axis	2nd PCA axis
	Chem.R	Mow.IR	Chem.R	Mow.IR	Chem.R	Mow.IR
	→ Till.	→	→ Till.	Mow.IR	→ Till.	Mow.IR
	IR, Till.R	Chem.IR + Till.IR	IR, Till.	→	IR, Till.	→
			Chem.	R	Chem.	R
			IR + Till.IR		IR + Till.IR	
Maximum height	0.02	-0.01	0.03	0.08	-0.1	0.07
SLA	0.09	0.11	-0.26	0.4*	-0.08	0.09
Seed mass	-0.06	-0.06	-0.07	0.02	-0.01	0.03
Lateral spread	0.45***	-0.19	0.17	0.08	-0.11	-0.03
Flowering onset	0.1	0.01	-0.12	0.38*	-0.19	0.03
Flowering duration	0.03	-0.11	-0.08	0.41*	-0.07	-0.09

et al. (2019). This method, widely applied on natural ecosystems, are still sparsely applied in agricultural contexts, especially in vineyards. We hypothesized that chemical weeding and tillage would act as stronger filters compared to mowing, and we expected that communities under chemical weeding and tillage would have convergent values of trait values with low variation. Half of the CWV had a significantly different distribution than random distribution and most of the CWV had convergent distribution. This demonstrates that regions, seasonality, year of survey and weed management practices impacted traits variabilities, mostly restricting the possible range of values of average trait values of weed communities. Moreover, it is likely that the assembly of species into communities in vineyards, which remains a disturbed environment, is also the result of neutral processes related to spatial colonization–extinction dynamics as shown in annual crop fields (Peronne et al., 2015). However, the separated analysis by region limited our statistical power and the results of our analysis should be interpreted with care.

### 4.1. Region and seasonality are the main drivers of the variation of community weighted means

Region was the main driver of traits related to resource acquisition (maximum height, SLA) and phenology (flowering onset and flowering duration) while season explained most of the variation of the regenerative traits (seed mass and lateral spread). According to our hypotheses, region and seasonality affected the functional structure of a community more than management practices.

Regional effects encompass different environmental effects, mostly differences in climate and soil characteristics. In the literature, the pedoclimatic effects on weed functional structures depend on the scale of studies. For instance, within the same wine-growing region in South Africa, MacLaren et al. (2019) found no significant effects of soil characteristics and climate on communities weighed means. In contrast, in several European countries, Hall et al. (2020) showed that the country effect was the main factor affecting traits. Within the same country, our study showed that divergent edaphoclimatic conditions between wine-growing regions had major impacts on traits.

More precisely, regional effects encompass the differences in climate between Languedoc, Rhône and Champagne and had contrasted effects on CWM of communities in Champagne (drier and colder climate) and communities in Languedoc (hotter climate). In Champagne, weed communities presented higher SLA values compared to Languedoc. This result is consistent with other studies at the individual scale showing that SLA was negatively correlated with mean annual temperature (Garnier et al., 2019; Moles et al., 2014; Wright et al., 2005, 2004) and positively with precipitation (Garnier et al., 2019). Indeed, plants with low SLA invest in the leaf structure to adapt to dry conditions (e.g. thick leaf blade to limit evapotranspiration; small and thick-walled cells) (Wright et al., 2005). On average, flowering onset was later in Languedoc compared to Champagne where most of the weed species flowered in spring. This could be explained by the bi-modality of the flowering period (Thompson, 2007) in Languedoc region. Two favourable periods are possible to flower: (i) early spring before the summer drought and (ii) early autumn after the first rainfalls (Kummerow, 1983; Thuiller et al., 2004). Due to higher temperatures in autumn, more thermophile species can flower and produce seeds during this season in the Mediterranean region (e.g. *Dittrichia viscosa*, *Heliotropium europaeum*, *Sorghum halepense*, *Tribulus terrestris*). Thus, on average, this could explain the later flowering communities of the Languedoc.

Moreover, soil characteristics are also encompassed in the regional effect. In our dataset, vineyard plots located in the Rhône had more fertile soils (high soil organic content) compared to vineyard plots of the other regions (Table A.1). Fertile soils are usually associated with weed communities with high photosynthetic assimilation rates, high SLA, high height at maturity and low seed mass (Garnier et al., 2016). However, only flowering duration was significantly different in the Rhône region while the other traits were not significantly different from the other regions.

In addition to different soils and climates, the regional effect might also include some management practices and technical characteristics that vary according to wine-growing regions: the amount of applied nutrients through fertilization and amendments, the density of vine stocks (higher density in Rhône than in Languedoc) or grape variety (Gamay and Syrah in Rhône, Cabernet Sauvignon and Grenache in Languedoc).

In addition to the regional effect, seasonality was the most frequently selected effect in the reduced models explaining CWM. Interestingly, Fried et al. (2019) found that season was the main driver of the taxonomic composition of weed community in vineyards. Surveyed autumn weed communities had higher maximum height, lower SLA, heavier seeds, high lateral spread abilities and later flowering onset than at other survey dates. This can be explained by the changes in environmental conditions throughout the growing seasons (Wolkovich and Cleland, 2014): in late winter, disturbance is high in the vineyards (first weeding passages) with non-limiting weather conditions (regular rainfall, increasing temperatures) selecting early-flowering species with rapid-growth and acquisitive strategies (high SLA, low stature, low seed mass) while in summer, disturbing events such as weeding are less frequent and weather conditions can lead to water stress or heat stress. Consequently, more stress-tolerant communities might develop during the summer drought with slow-growth and more conservative strategies (low SLA, high stature, high weight seeds).

#### 4.2. Soil disturbance gradient: soil tillage versus chemical weeding

The first PCA axis of weed management practices and temporal variables (seasonality and year of floristic surveys) represented the soil disturbance gradient from tilled soils with high below-ground mechanical disturbances to chemically weeded soils with no below-ground mechanical disturbance.

According to our hypotheses, chemical weeding on rows was associated to most of the trait values characterizing ruderal communities (low seed mass, short stature in Champagne, low lateral spread, early

flowering). However, SLA was not significantly higher in chemically weeded communities than in tilled communities. Moreover, communities from chemically weeded plots in the Rhône had high stature which is not an expected trait value of ruderal strategy communities. In contrast to our hypotheses, tillage seemed to favour weed communities with high seed mass which is inconsistent with the trait values of ruderal communities. Different mechanisms could explain these contrasted trait values between these two types of weed management. One possible explanation relates to the changes of seed positions in the soil which depend on the different weed management practices. Indeed, chemical weeding associated to no-till practices favours superficial position of seeds, whereas tillage commonly buries the seeds deeper into the soil. Unburied seeds are more likely to be eliminated by predation or impaired by desiccation. Therefore, under chemical weeding, producing a large number of low weight seeds might increase the probability that some of them survive. On the contrary, large and high weight seeds have a greater probability to germinate when they are buried (Benvenuti et al., 2001; Hernández Plaza et al., 2015; MacLaren et al., 2019). Under superficial tillage practices (as here in vineyards), large-seeded community have been found in several studies in line with our results (Armengot et al., 2016; Hernández Plaza et al., 2015; MacLaren et al., 2019).

Moreover, tillage is a soil disturbance (Gaba et al., 2014) that selects annual species with a seedbank but also species that can regenerate from fragments such as rhizome species (e.g. *Convolvulus arvensis* or *Cirsium arvense*) with high lateral spread abilities as highlighted here in two regions (Languedoc and Champagne). Tillage was also associated to high variability of lateral spread values within communities. Thus, tillage seemed to favour two different strategies (Fig. A.17): the main strategy would be the ability to re-sprout using vegetative multiplication after tillage (high lateral spread communities). The second minor strategy would be similar to chemically weeded communities: short life cycle communities with low lateral spread abilities.

#### 4.3. Vegetation cover gradient: mowing versus tillage and chemical weeding

In contrast to Fried et al. (2019) findings on taxonomic composition, mowing has here been found to be a major driver of functional structure of weed communities in the Languedoc. Vegetation abundance (i.e. the sum of the abundance of each species per plot) in mowed inter-rows were much higher than in chemically weeded and/or tilled inter-rows (Fried et al., 2019). The weeding practice gradient from chemical weeding and tillage to mowing can therefore be interpreted as vegetation cover gradient from bare soils (tillage and chemical weeding) to high vegetation cover (mowing) (Hall et al., 2020).

Interestingly, the combination of chemical weeding and tillage on inter-rows seemed to favour ruderal communities in Languedoc (short-stature, high SLA, low seed mass, low lateral spread abilities and early flowering) and were opposed to more competitive communities on mowed inter-rows. In Languedoc, mowing was associated to rosette plants like *Lactuca serriola*, *Crepis vesicaria* and *Torilis arvensis* which can reach 67 cm to more than 1.5 m height. The sequential application of a belowground (soil tillage) and an aboveground (herbicides) action thus act as a severe disturbance for vegetation. It may select species with a rapid life-cycle that flower early to escape disturbances, have a high acquisitive strategy (high SLA), a low investment in vegetative parts (low maximum height) and a massive production of low weight seeds to increase the probability that some survive (Grime, 1977; White and Pickett, 1985).

In contrast, mowing was associated with late flowering species communities compared to chemical weeding and tillage in the Rhône. This could be explained by the timing of weed management practices. Indeed, mowing is generally carried out later than the other weed management practices: early July on average for mowing, May for chemical weeding and for tillage in the Rhône (Table 1).

We expected that highly disturbed rows and inter-rows such as tilled and chemically weeded rows would lead to a reduction in the range of trait values (convergent distributions) compared to mowed rows and inter-rows (divergent distributions) (Kazakou et al., 2016). In contrast with our expectations, combined tillage and chemical weeding were associated with high CWV of SLA, flowering onset and duration while mowing was associated to more convergent distributions in Champagne. A possible explanation is that chemical weeding and tillage select contrasted strategies (e.g., geophytes with high lateral spread and therophytes) leading to higher variability of trait values when combining them (Fig. A.17).

#### 4.4. Limits and perspectives

Trait-based approaches are promising a better understanding of the functional shaping of weed communities by weed management practices. In our study, the lateral spread ability of communities was certainly one of the major response traits. Other traits, absent from the databases, such as the presence of epicuticular wax on leaves or seed coat thickness, might be response traits of interest to include in such studies where herbicide pressure is an important filter (Gaba et al., 2014). However, these specific traits are still lacking in trait databases.

The use of pluriannual database of floristic surveys such as the Biovigilance network is an asset when considering the variations between years due to changing climatic conditions for instance. Moreover, the wide geographic range of our study allowed us to analyse the different weed management practices within regions and different pedoclimatic contexts. At this large-scale of analysis, one drawback is that we had to fragment the dataset to control the weed management and pedoclimatic contexts interactions therefore limiting the statistical power of our dataset. Another disadvantage is that it is difficult to use measured trait values. We therefore used database trait values based on the assumption that the ranking of species according to their trait values is stable across environments ('stable species hierarchy', Kazakou et al., 2014) as interspecific variability is higher than intraspecific variability. A recent study has shown that this hypothesis was largely valid in vineyards (Garcia et al., 2020).

Another point is that our results demonstrated that weed management practices explained 19% of variations of functional structure of weed communities. More detailed variables describing management practices could help better understand plant responses, for instance considering disturbance types such as frequency (e.g. number of applied management practices within a year) and intensity (e.g. herbicide dose or depth of tillage) (Gaba et al., 2014). For instance, the timing of weed management practices has been shown to be relevant to explain functional responses of weed communities (Cordeau et al., 2017; Smith, 2006).

## 5. Conclusion

In this paper, we have shown that the changes in composition of weed species caused by environmental and anthropogenic filters in vineyards also lead to changes in functional structure. Region, seasonality and weed management practices act as strong drivers of functional structure of weed communities. Weed management practices impacted both the mean trait values and their variance within weed communities. Chemically weeded communities shared most of the trait values of ruderal strategies (low seed mass, small-stature, early flowering, short lateral spread abilities). Weed communities from mowed plots were associated with more competitive strategies (higher seed mass, higher stature and lower SLA). Tillage favoured communities with high seed mass which increases the viability of buried seeds and high lateral spread abilities values related to the capacity to resprout after tillage. Nowadays, mowing and tillage are more and more applied in vineyards (Simonovici, 2019). Our results showed that this soil management shift might favour more competitive communities. These weed communities

might also have different impacts on agrosystem processes such as nitrogen cycling or carbon sequestration through changes in soil microbial composition (Karimi et al., 2020). Understanding the effect of weed communities on such processes is needed to adapt weed management practices and better drive ecosystem services and disservices (Damour et al., 2018; Garcia et al., 2018; Petit et al., 2018; Storkey et al., 2015).

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.107892.

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## SUPPLEMENTARY MATERIAL

**Table A.1** Number of surveyed vineyard plots per year and per season in Champagne, Languedoc and Rhône.

<b>Years</b>	<b>Season</b>	<b>Champagne</b>	<b>Languedoc</b>	<b>Rhône</b>
2006	Autumn	-	10	14
2007	Spring	-	6	15
	Summer	-	-	-
	Autumn	-	6	15
2008	Spring	-	18	15
	Summer	-	-	-
	Autumn	-	18	15
2009	Spring	-	13	10
	Summer	-	-	-
	Autumn	-	13	12
2010	Spring	5	9	10
	Summer	5	-	4
	Autumn	1	9	12
2011	Spring	9	-	-
	Summer	9	-	-
	Autumn	-	-	-
2012	Spring	8	-	-
	Summer	8	-	-
	Autumn	1	-	-
Number of floristic surveys		46	102	122
Total number of plots		10	18	18

**Table A.2** Climate and soil characteristics for each wine-growing region. Climate characteristics data have been extracted from the WorldClim database (Hijmans et al., 2005). Soil characteristics data have been extracted from the Soilgrids dataset at 250 m resolution (Hengl et al., 2017) based on the locations of vineyard plots.

<b>Climate and soil variables</b>	<b>Champagne</b>	<b>Languedoc</b>	<b>Rhône</b>
<b>Climate</b>			
Mean annual temperature (°C)	10.1	14.1	11.4
Annual rainfall (mm)	657	686	776
<b>Soil</b>			
Soil organic carbon content (%)	16.5 +/- 2.5	16.4 +/- 1.3	19.7 +/- 1.9
pH index measured in water solutions	7.1 +/- 0.1	7.5 +/- 0.1	6.7 +/- 0.3
Cation-exchange capacity	17.4 +/- 1	16.1 +/- 1.4	17 +/- 2.1
Bulk density (fine heart) (kg/m <sup>3</sup> )	1387.3 +/- 21.7	1527.6 +/- 14.7	1473 +/- 28.2
Volumetric percentage of coarse fragments (> 2 mm) (%)	13.2 +/- 1.2	12.5 +/- 2.1	13 +/- 1.2
Weight percentage of sand particles (0.05 – 2 mm) (%)	30.4 +/- 3.8	33.7 +/- 2	36.7 +/- 3.7
Weight percentage of silt particles (2.10 <sup>-4</sup> – 0.05 mm) (%)	45.7 +/- 3.6	38.9 +/- 1.2	37.7 +/- 2.2
Weight percentage of clay particles (< 2.10 <sup>-4</sup> mm) (%)	23.6 +/- 1.8	27.4 +/- 2.1	25.5 +/- 2

**Table A.3** Contributions of explaining variables to the PCA of weed management practices and temporal variables (Figure 4). D, number of days since the 1<sup>st</sup> January of the same year

	<b>Contribution to axis 1</b>	<b>Contribution to axis 2</b>
	<b>(%)</b>	<b>(%)</b>
Till.R	75	1
Chem.R	64	4
Till.IR	48	19
Chem.IR	18	42
Mow.IR	7	87
Years	4	5
D	3	2

**Table A.4** Akaike Information Criterion (AIC), the percentage of variance explained by fixed effect ( $R_{\text{marg}}$ ) and by fixed and random effects ( $R_{\text{cond}}$ ) of each CWM model. The full model was :  $\text{CWM} \sim \text{Region} + \text{Seasonality} + \text{Chem.IR} + \text{Till.IR} + \text{Mow.IR} + \text{Chem.R} + \text{Till.R} + (1|\text{Year}) + (1|\text{Plot})$

Community weighted means	AIC		$R_{\text{marg}}$		$R_{\text{cond}}$	
	Null model	Parsimonious model	Null model	Parsimonious model	Null model	Parsimonious model
Maximum Height CWM	-54	-75	30	29	41	39
SLA CWM	1319	1317	31	29	42	39
Log(Seed mass CWM)	622	609	17	15	39	35
Log(Lateral spread CWM)	167	143	10	13	51	50
Flowering onset CWM	735	719	35	35	49	49
Flowering duration CWM	-9	-52	48	48	62	61

**Table A.5** Means and standard deviations of community weighted means for each region. Cha, Champagne ; Lan, Languedoc ; Rhône, Rhône ; Sd, standard deviation.

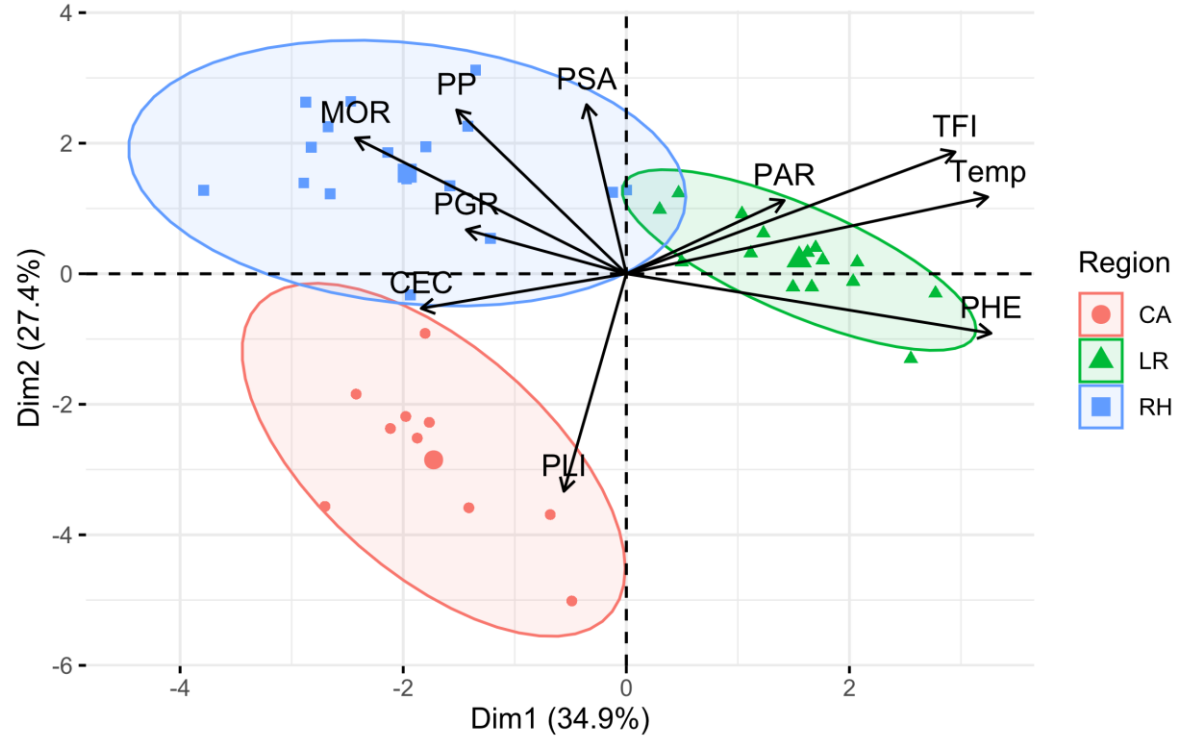
Region	SLA CWM (mm <sup>2</sup> /mg)		Maximum height CWM (m)		Seed mass CWM (g)		Flowering onset CWM (months)		Flowering duration CWM (months)		Lateral spread CWM	
	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd
Cha	30,0	3,1	0,73	0,16	1,41 0 <sup>-03</sup>	7,01 0 <sup>-04</sup>	3,3	0,9	8,1	1,4	1,63	0,47
Lan	24,4	2,9	0,98	0,24	3,21 0 <sup>-03</sup>	3,91 0 <sup>-03</sup>	4,8	0,9	4,5	1,0	1,81	0,90
Rhône	26,7	3,6	0,80	0,20	1,81 0 <sup>-03</sup>	1,81 0 <sup>-03</sup>	4,1	1,1	6,3	1,7	1,65	0,58



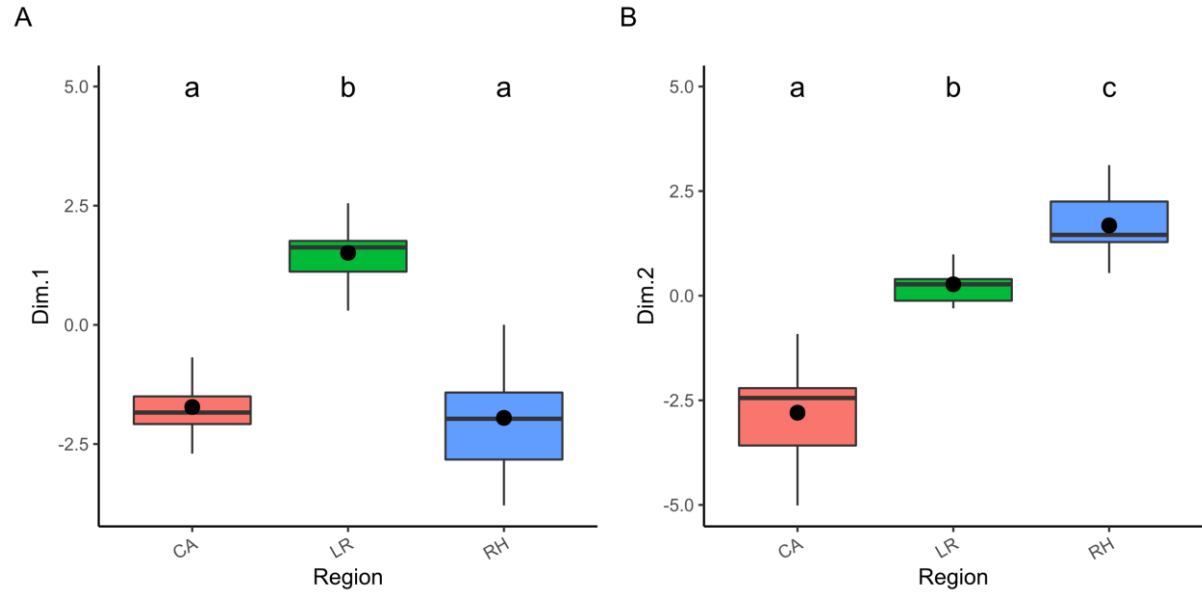
**Table A.6** Means and standard deviations of community weighted variance for each region. Cha, Champagne ; Lan, Languedoc ; Rhône, Rhône ; Sd, standard deviation

Region	SLA CWV (mm <sup>2</sup> /mg)		Maximum height CWV (m)		Seed mass CWV (g)		Flowering onset CWV (months)		Flowering duration CWV (months)		Lateral spread CWV	
	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd
Cha	43,0	27,8	0,15	0,11	9,41 0-06	1,31 0-05	3,5	1,9	9,5	4,3	0,88	0,67
Lan	23,3	17,7	0,15	0,09	2,91 0-04	8,61 0-04	1,6	0,9	3,9	3,9	1,47	1,25
Rhône	33,9	22,0	0,13	0,08	1,31 0-05	2,81 0-05	2,8	1,7	7,0	4,2	1,24	1,02

**Fig. A.1** Projection of vineyard plots from different regions within the soil-climate gradient of the dataset. MOR, Organic Matter ; PHE, pH index measured in water solutions ; CEC, Cation-exchange capacity ; TFI, Bulk density (fine heart) ; PGR, Volumetric percentage of coarse fragments ; PL, weight percentage of silt particles ( $2 \cdot 10^{-4} - 0.05 \text{ mm}$ ) ; PSA, weight percentage of sand particles ( $0.05 - 2 \text{ mm}$ ) ; PAR, Weight percentage of clay particles ( $< 2 \cdot 10^{-4} \text{ mm}$ ) ; Temp, mean annual temperature ; PP, Annual rainfall ; CA, Champagne ; LR, Languedoc Roussillon ; RH, Rhône Valley.



**Fig. A.2** Comparison of the coordinates of the plots in the first (A) and the second (B) axis of soil-climate PCA. CA, Champagne ; LR, Languedoc Roussillon ; RH, Rhône Valley. Kruskal-Wallis tests were performed to compare the means of the coordinates.



**Fig. A.3** Significant associations of the fourth-corner tests between the first two RLQ axes and the agro-environmental variables (a) and the species traits (b). Green boxes show positive correlations and red boxes negative correlations. Significance of associations are referred as following: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ; ns, non-significant ( $p > 0.05$ ).

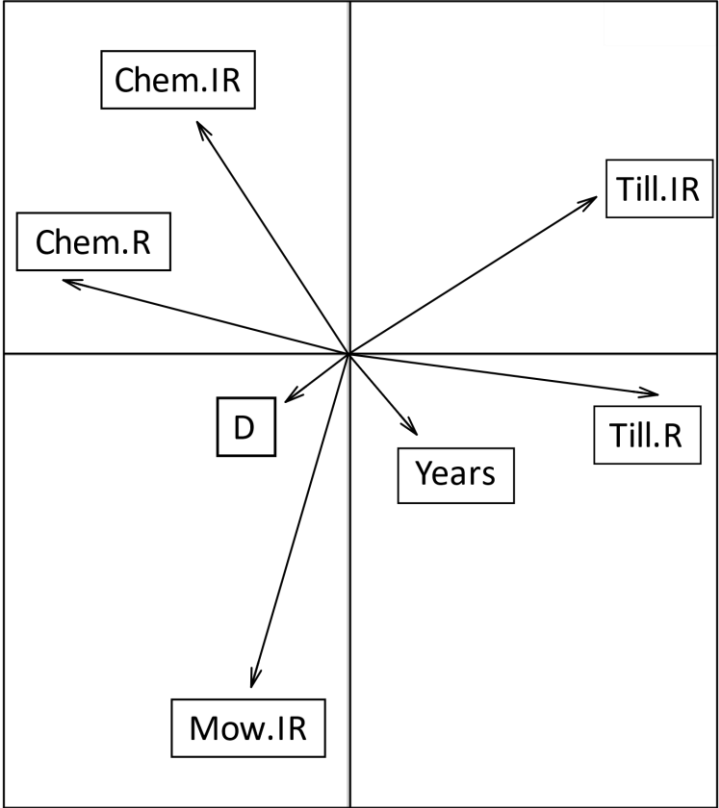
(a)

	RLQ Axis 1	RLQ Axis 2
Champagne	*	ns
Languedoc	**	ns
Rhône	ns	ns
Seasonality	*	*
Years	*	ns
Chem.IR	*	*
Mow.IR	*	ns
Till.IR	**	ns
Chem.R	*	**
Till.R	*	*

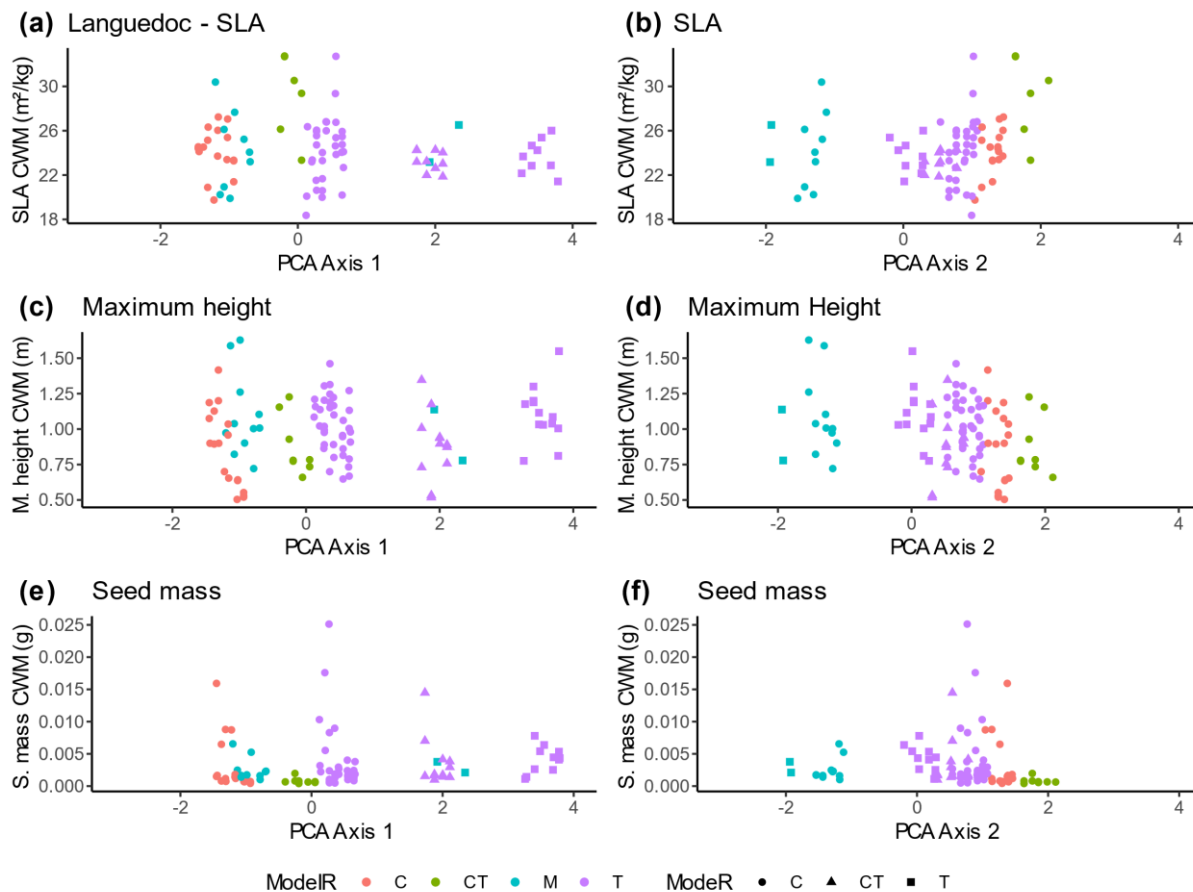
(b)

	RLQ Axis 1	RLQ Axis 2
Maximum height	***	ns
SLA	***	ns
Seed mass	ns	*
Flowering onset	***	ns
Flowering duration	***	*
Lateral spread	*	*

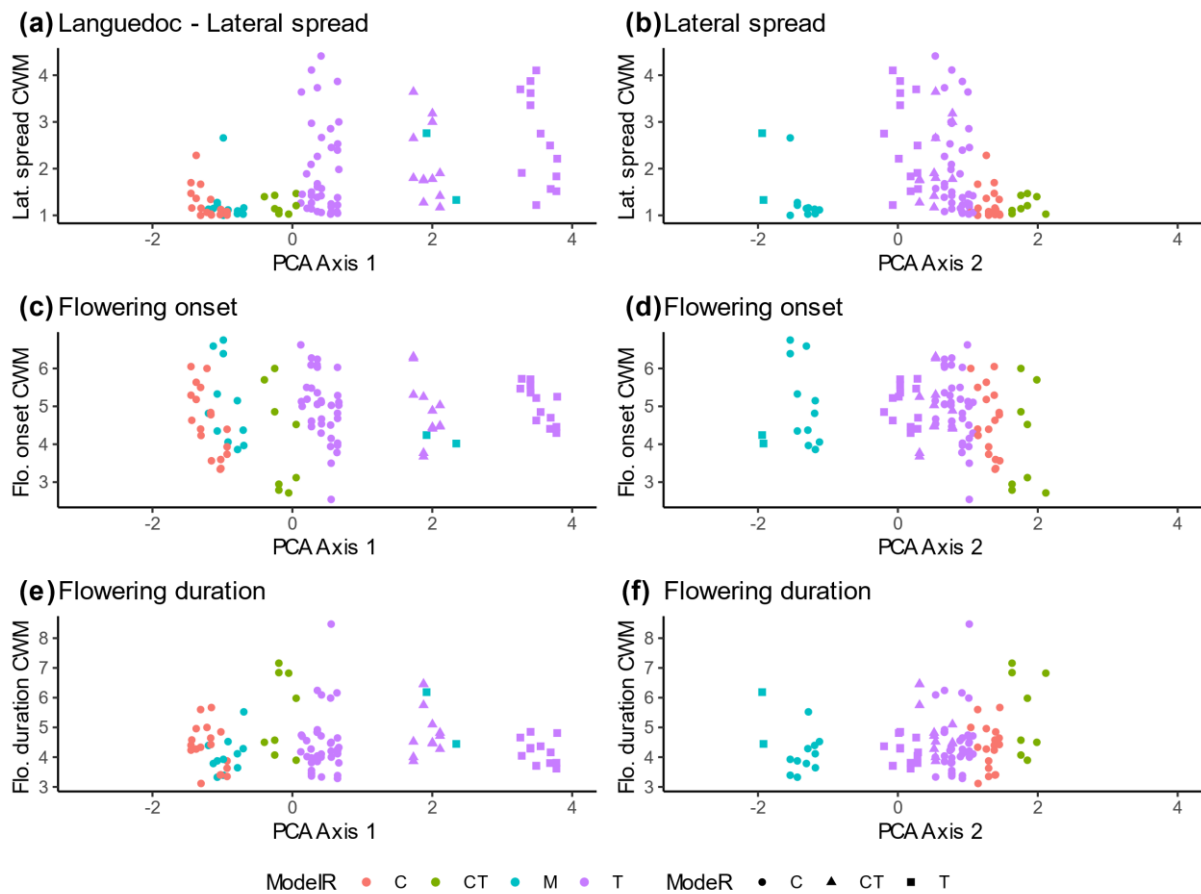
**Fig. A.4** Display of temporal and weed management practices variables along the first two PCA axes. *D*, seasonality (number of days since the beginning of the year of floristic survey ; *Years*, year of floristic survey. For the abbreviations of weed management practices, see Table 1.



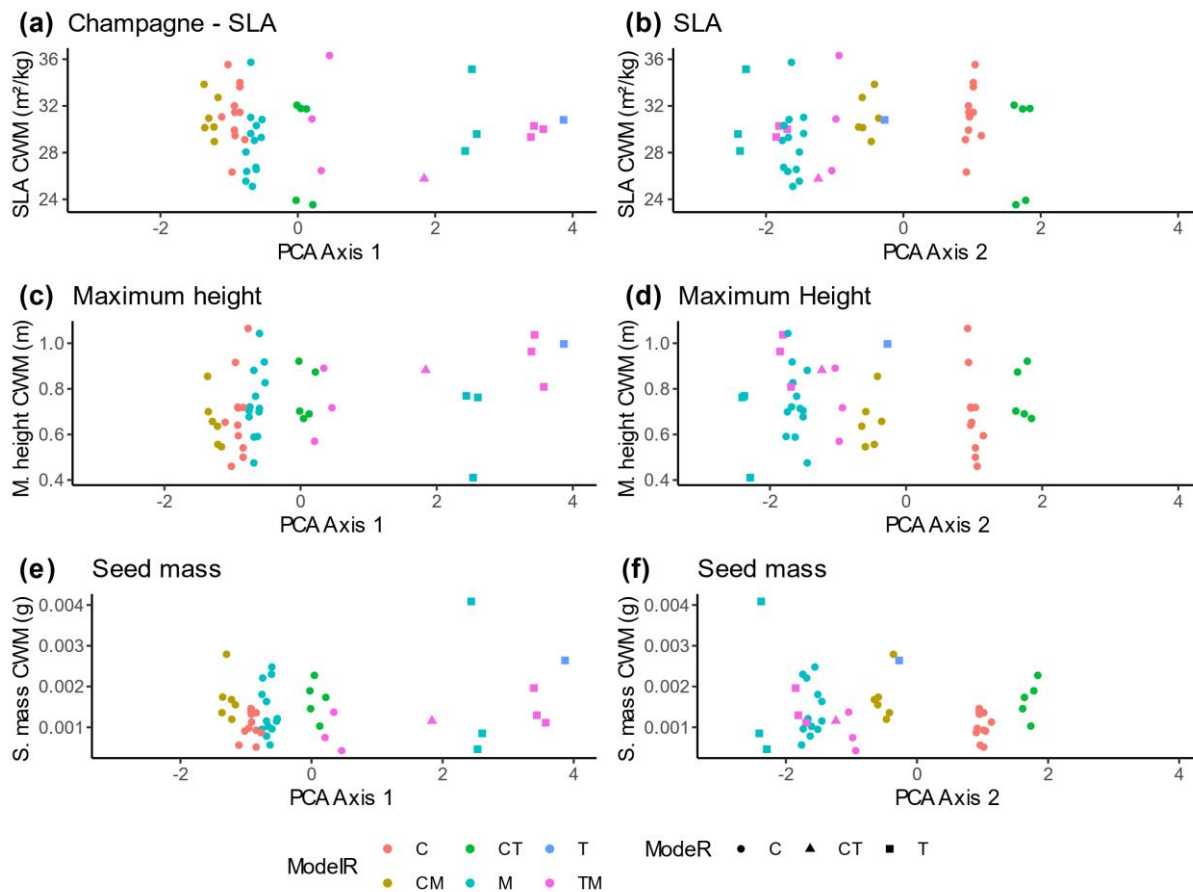
**Fig. A.5** Community Weighted Means (CWM) along the first two axes of the weed management practices and temporal variables PCA (Figure 4) in Languedoc. The SLA CWM, maximum height CWM, seed mass CWM of weed community are displayed along the first PCA axis (a, c, e) and along the second PCA axis (b, d, f) respectively. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates,) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). Each point is a weed community. The color of each point specify the weed management of inter-rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; M, mowing ; T, Tillage). The shape indicate the weed management of rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; T, Tillage).



**Fig. A.6** Community Weighted Means (CWM) along the first two axes of the weed management practices and temporal variables PCA (Figure 4) in Languedoc. The lateral spread CWM, flowering onset CWM, flowering duration CWM of weed community are displayed along the first PCA axis (a, c, e) and along the second PCA axis (b, d, f) respectively. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates,) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). Each point is a weed community. The color of each point specify the weed management of inter-rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; M, mowing ; T, Tillage). The shape indicate the weed management of rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; T, Tillage).

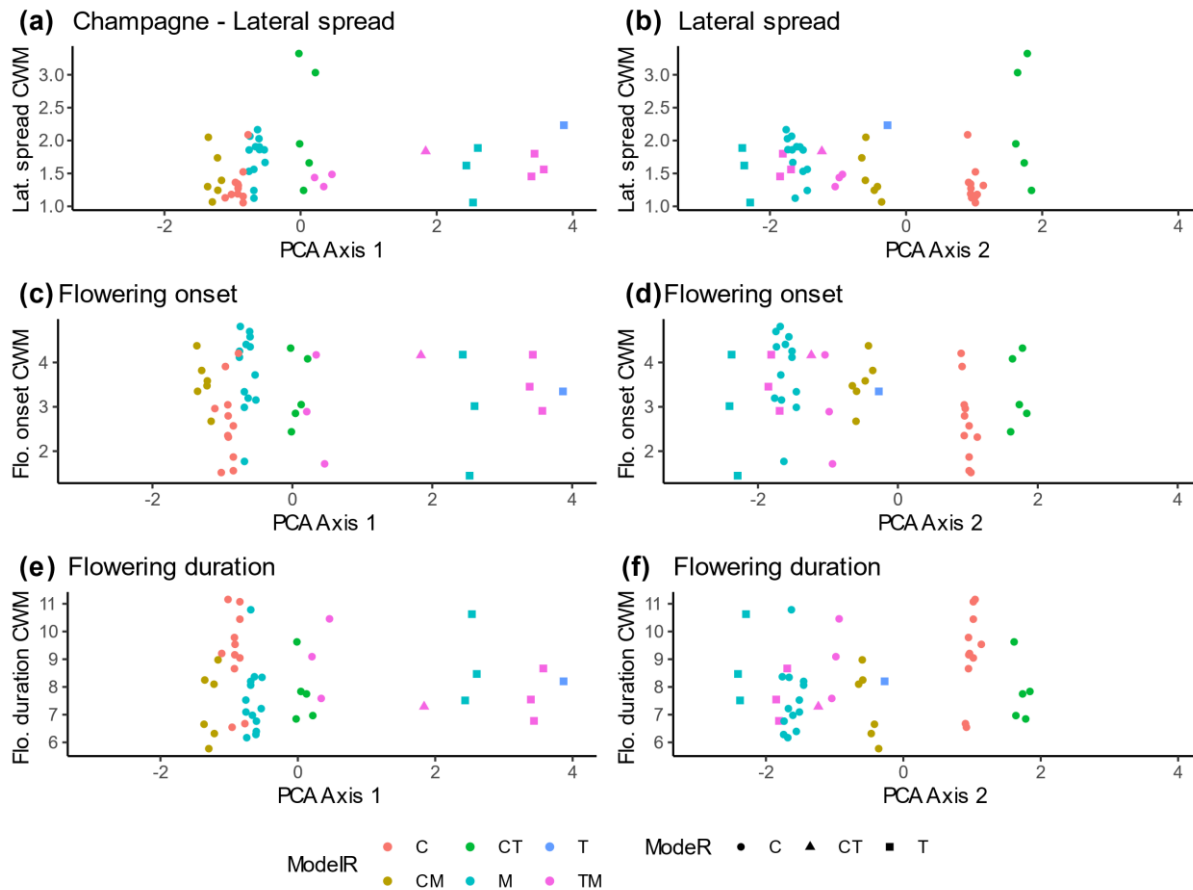


**Fig. A.7** Community Weighted Means (CWM) along the first two axes of the weed management practices and temporal variables PCA (Figure 4) in Champagne. The SLA CWM, maximum height CWM, seed mass CWM of weed community are displayed along the first PCA axis (a, c, e) and along the second PCA axis (b, d, f) respectively. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates,) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). Each point is a weed community. The color of each point specify the weed management of inter-rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; CM, combination of chemical weeding and mowing ; TM, combination of tillage and mowing ; M, mowing ; T, Tillage). The shape indicate the weed management of rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; T, Tillage).

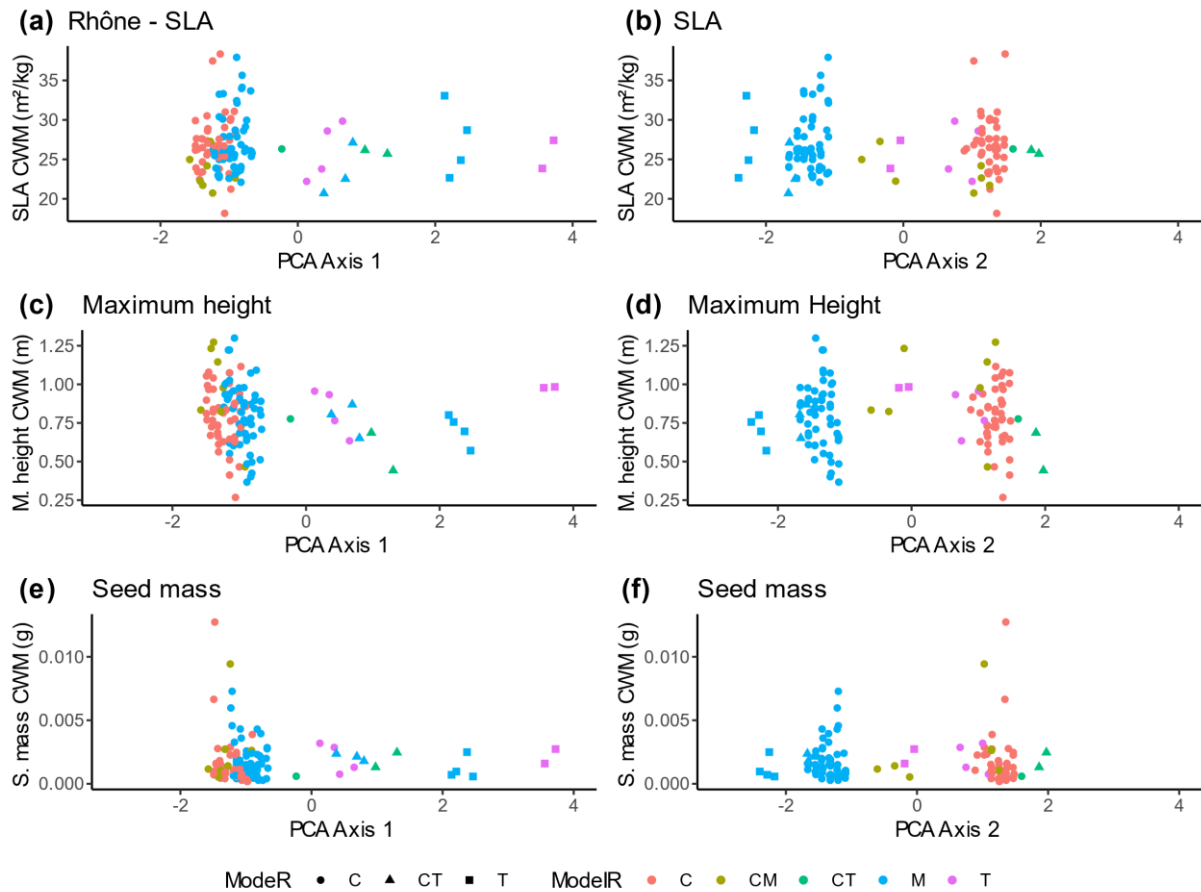




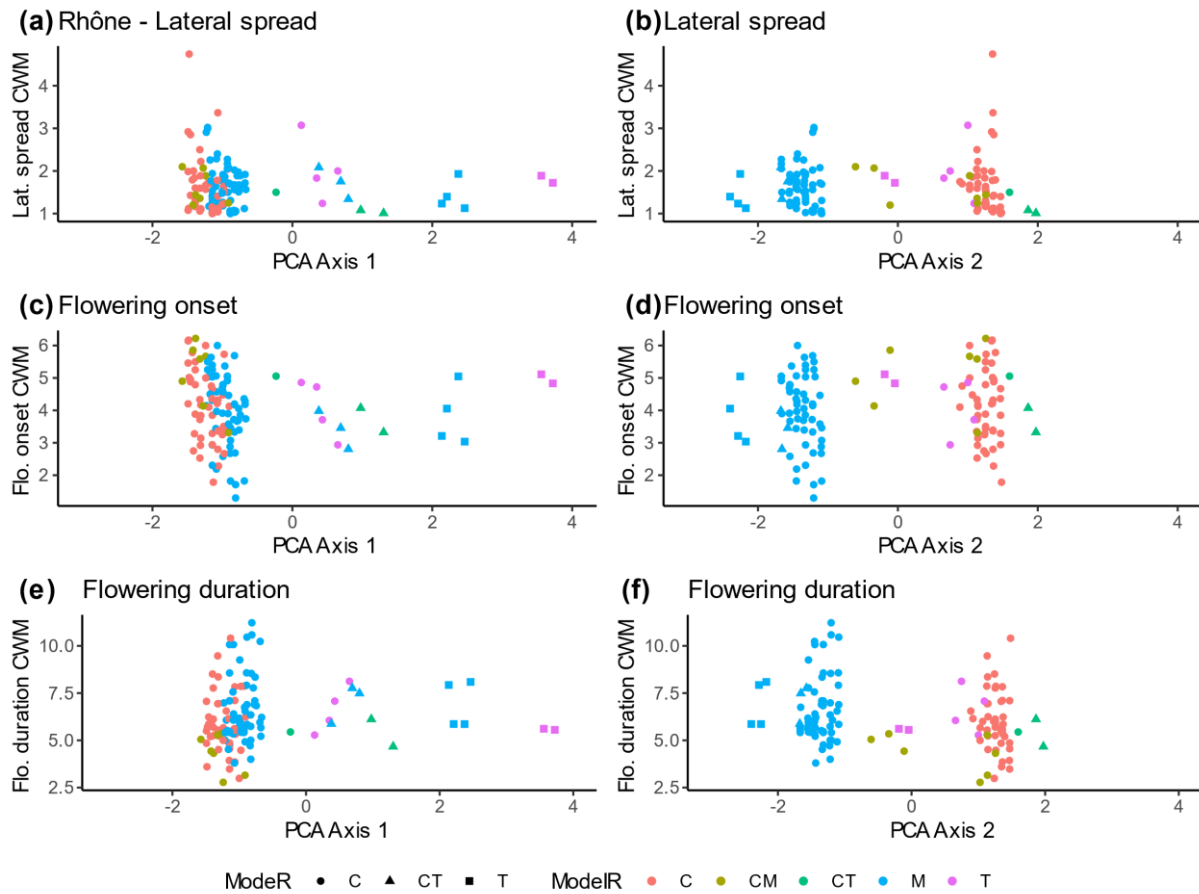
**Fig. A.8** Community Weighted Means (CWM) along the first two axes of the weed management practices and temporal variables PCA (Figure 4) in Champagne. The lateral spread CWM, flowering onset CWM, flowering duration CWM of weed community are displayed along the first PCA axis (a, c, e) and along the second PCA axis (b, d, f) respectively. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates,) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). Each point is a weed community. The color of each point specify the weed management of inter-rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; CM, combination of chemical weeding and mowing ; TM, combination of tillage and mowing ; M, mowing ; T, Tillage). The shape indicate the weed management of rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; T, Tillage).



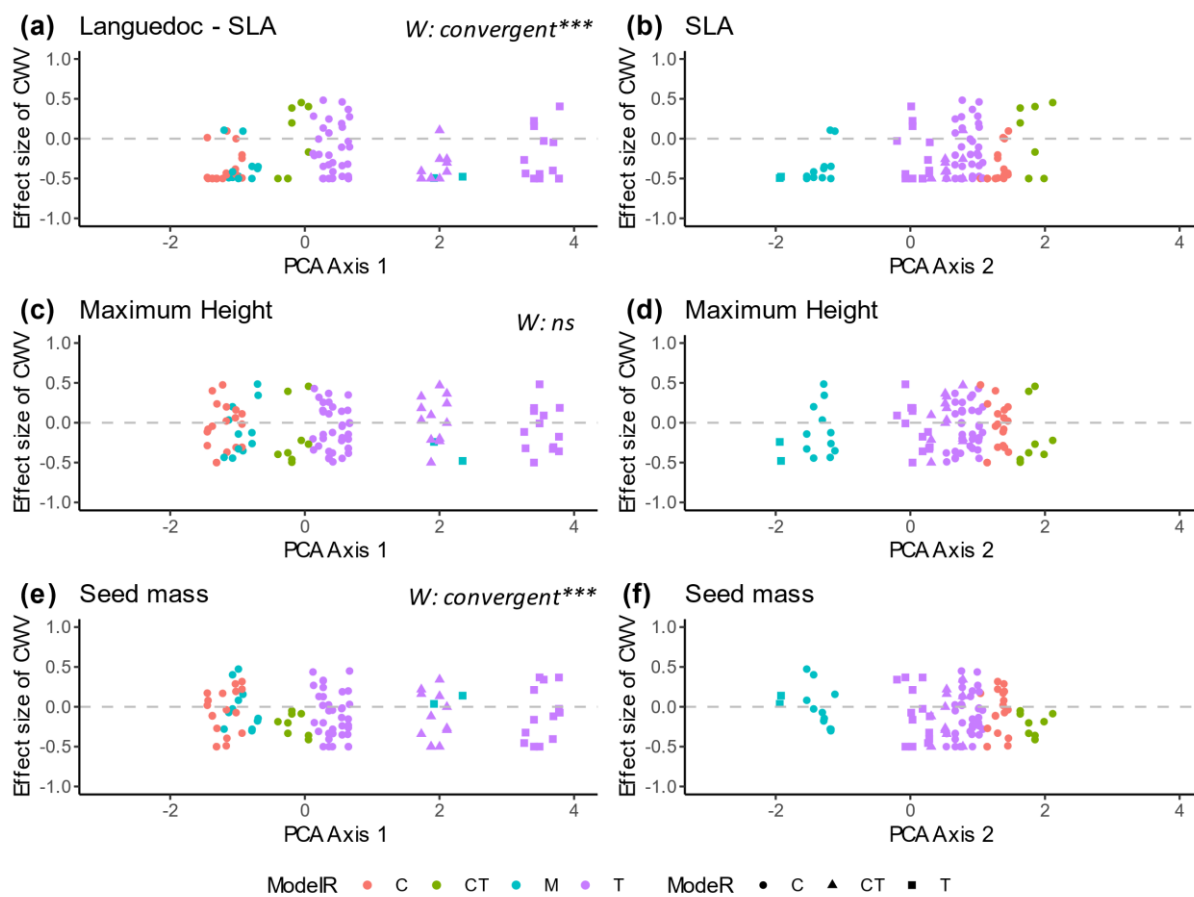
**Fig. A.9** Community Weighted Means (CWM) along the first two axes of the weed management practices and temporal variables PCA (Figure 4) in Rhône. The SLA CWM, maximum height CWM, seed mass CWM of weed community are displayed along the first PCA axis (a, c, e) and along the second PCA axis (b, d, f) respectively. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates,) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). Each point is a weed community. The color of each point specify the weed management of inter-rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; CM, combination of chemical weeding and mowing ; M, mowing ; T, Tillage). The shape indicate the weed management of rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; T, Tillage).



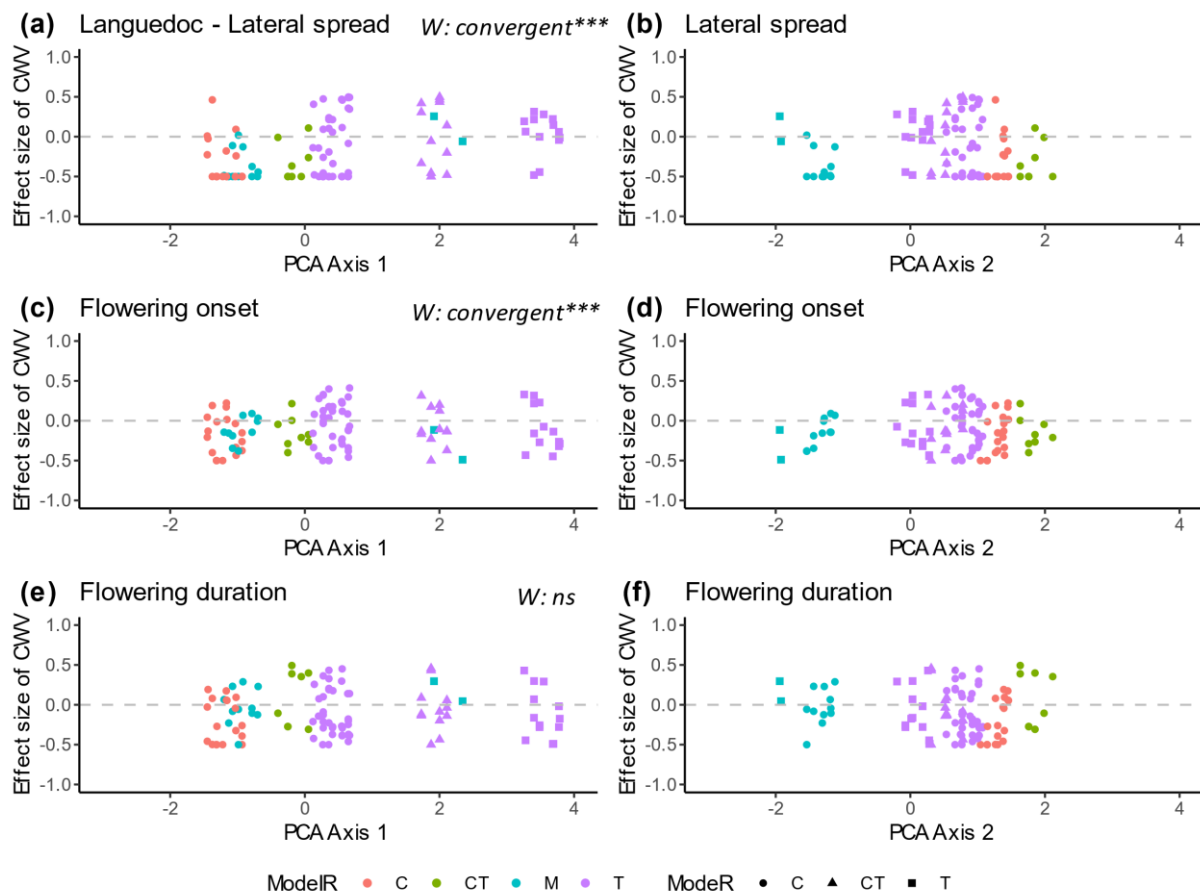
**Fig. A.10** Community Weighted Means (CWM) along the first two axes of the weed management practices and temporal variables PCA (Figure 4) in Rhône. The lateral spread CWM, flowering onset CWM, flowering duration CWM of weed community are displayed along the first PCA axis (a, c, e) and along the second PCA axis (b, d, f) respectively. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates,) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). Each point is a weed community. The color of each point specify the weed management of inter-rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; CM, combination of chemical weeding and mowing ; M, mowing ; T, Tillage). The shape indicate the weed management of rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; T, Tillage).



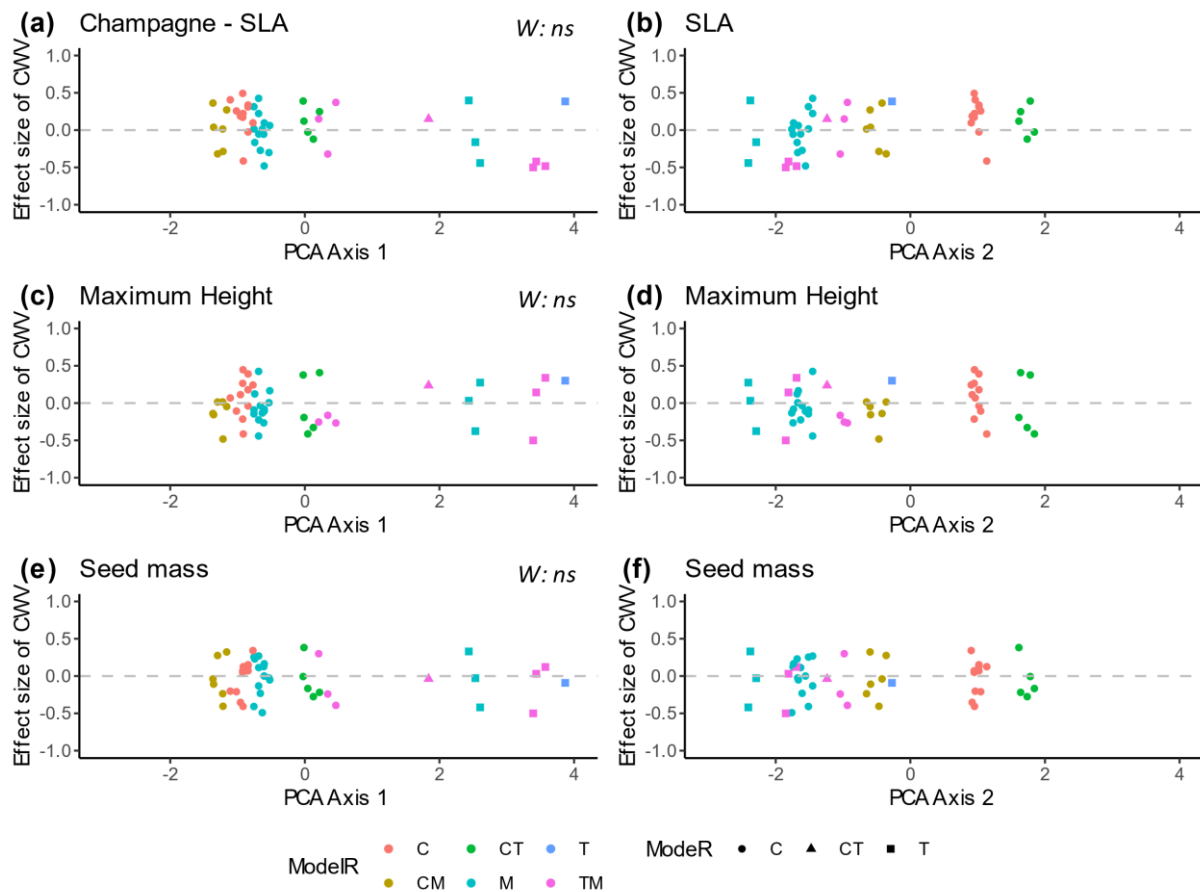
**Fig. A.11** Effect sizes of Community Weighted Variance (CWV) along the first two axes of the weed management practices and temporal variables PCA (Figure 4) in Languedoc. The effect size of SLA CWV, maximum height CWV and seed mass CWV of weed community are displayed along the first PCA axis (a, c, e) and along the second PCA axis (b, d, f) respectively. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates,) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). Each point is a weed community. The color of each point specify the weed management of inter-rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; M, mowing ; T, Tillage). The shape indicate the weed management of rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; T, Tillage). The results of the two-tailed Wilcoxon signed-ranks test (*W*) is specified. High and low ES values quantify respectively divergent and convergent functional structure of weed communities. Significance of Wilcoxon tests are referred as following: \*  $p < 0.05$  ; \*\*  $p < 0.01$  ; \*\*\*  $p < 0.001$ , ns ; non significant.



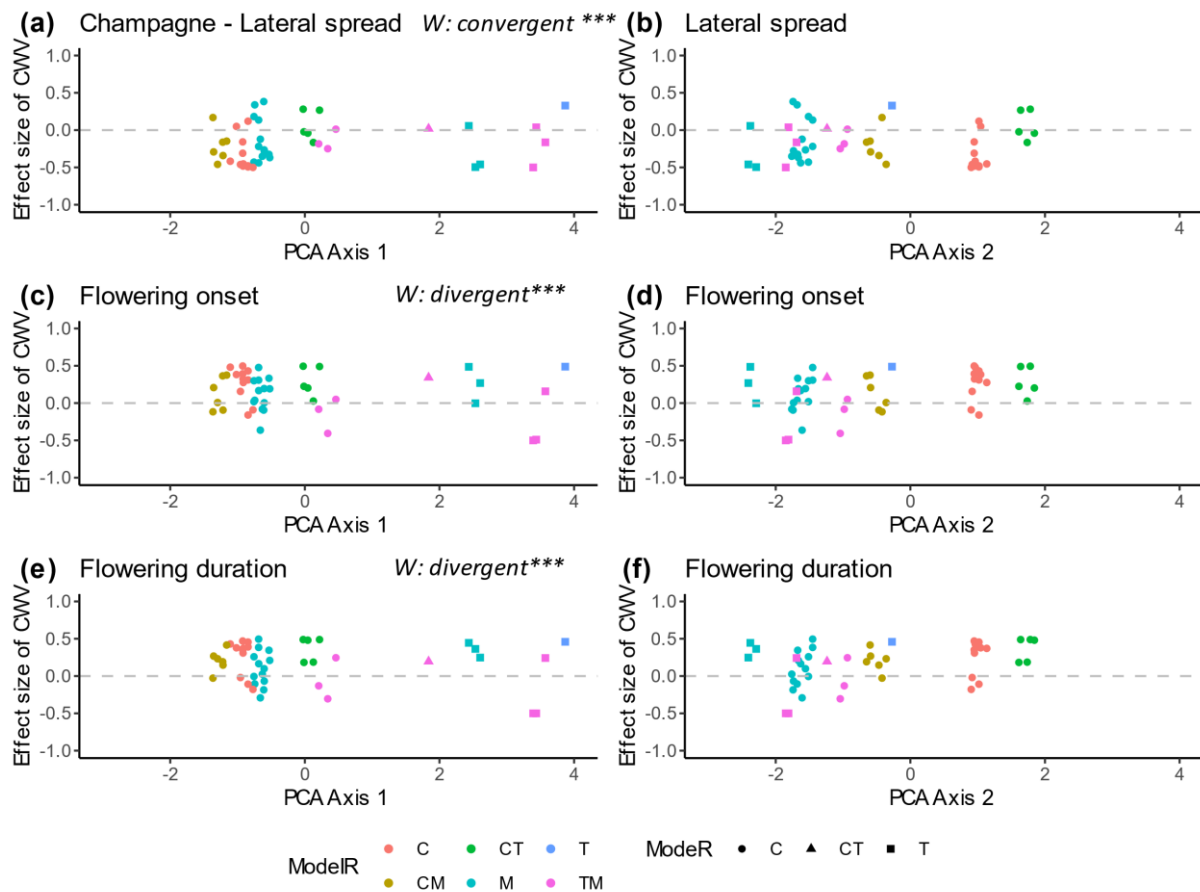
**Fig. A.12** Effect sizes of Community Weighted Variance (CWV) along the first two axes of the weed management practices and temporal variables PCA (Figure 4) in Languedoc. The effect size of lateral spread CWV, flowering onset CWV and flowering duration CWV of weed community are displayed along the first PCA axis (a, c, e) and along the second PCA axis (b, d, f) respectively. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates,) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). Each point is a weed community. The color of each point specify the weed management of inter-rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; M, mowing ; T, Tillage). The shape indicate the weed management of rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; T, Tillage). The results of the two-tailed Wilcoxon signed-ranks test ( $W$ ) is specified. High and low ES values quantify respectively divergent and convergent functional structure of weed communities. Significance of Wilcoxon tests are referred as following: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ , ns ; non significant.



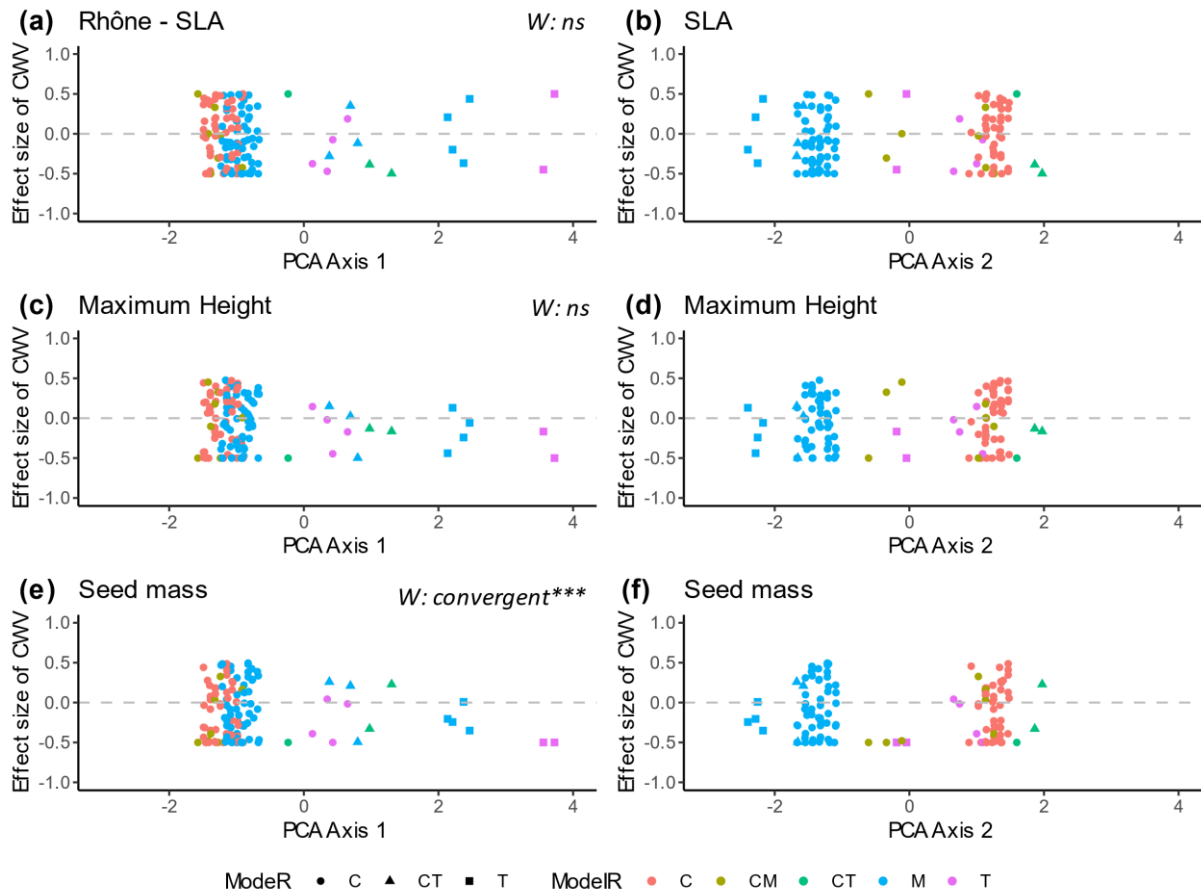
**Fig. A.13** Effect sizes of Community Weighted Variance (CWV) along the first two axes of the weed management practices and temporal variables PCA (Figure 4) in Champagne. The effect size of SLA CWV, maximum height CWV and seed mass CWV of weed community are displayed along the first PCA axis (a, c, e) and along the second PCA axis (b, d, f) respectively. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates,) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). Each point is a weed community. The color of each point specify the weed management of inter-rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; M, mowing ; T, Tillage). The color of each point specify the weed management of inter-rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; CM, combination of chemical weeding and mowing ; TM, combination of tillage and mowing ; M, mowing ; T, Tillage). The results of the two-tailed Wilcoxon signed-ranks test ( $W$ ) is specified. High and low ES values quantify respectively divergent and convergent functional structure of weed communities. Significance of Wilcoxon tests are referred as following: \*  $p < 0.05$  ; \*\*  $p < 0.01$  ; \*\*\*  $p < 0.001$ , ns ; non significant.



**Fig. A.14** Effect sizes of Community Weighted Variance (CWV) along the first two axes of the weed management practices and temporal variables PCA (Figure 4) in Champagne. The effect size of lateral spread CWV, flowering onset CWV and flowering duration CWV of weed community are displayed along the first PCA axis (a, c, e) and along the second PCA axis (b, d, f) respectively. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates,) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). Each point is a weed community. The color of each point specify the weed management of inter-rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; CM, combination of chemical weeding and mowing ; TM, combination of tillage and mowing ; M, mowing ; T, Tillage). The shape indicate the weed management of rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; T, Tillage). The results of the two-tailed Wilcoxon signed-ranks test (*W*) is specified. High and low ES values quantify respectively divergent and convergent functional structure of weed communities. Significance of Wilcoxon tests are referred as following: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ , ns ; non significant.

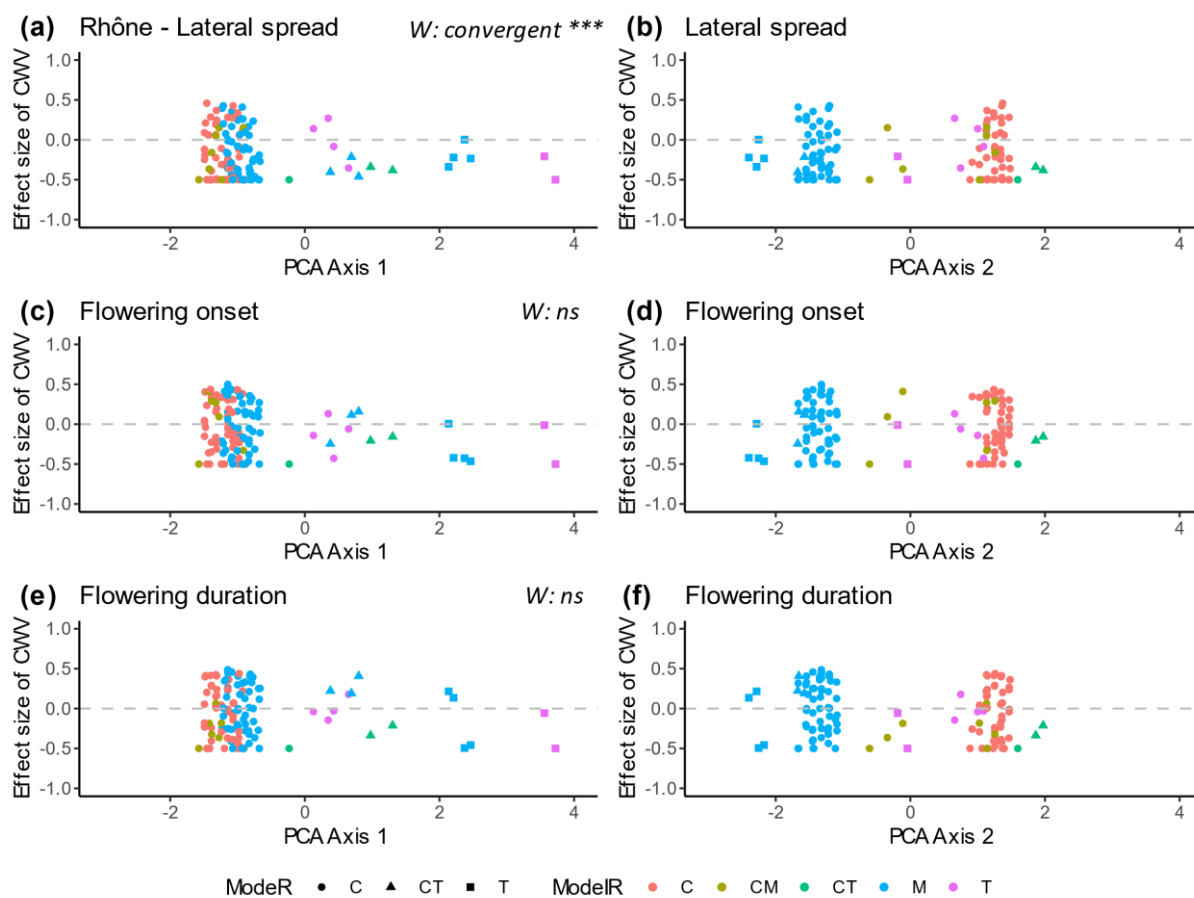


**Fig. A.15** Effect sizes of Community Weighted Variance (CWV) along the first two axes of the weed management practices and temporal variables PCA (Figure 4) in Rhône. The effect size of SLA CWV, maximum height CWV and seed mass CWV of weed community are displayed along the first PCA axis (a, c, e) and along the second PCA axis (b, d, f) respectively. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates,) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). Each point is a weed community. The color of each point specify the weed management of inter-rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; M, mowing ; T, Tillage). The color of each point specify the weed management of inter-rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; CM, combination of chemical weeding and mowing ; M, mowing ; T, Tillage). The results of the two-tailed Wilcoxon signed-ranks test (*W*) is specified. High and low ES values quantify respectively divergent and convergent functional structure of weed communities. Significance of Wilcoxon tests are referred as following: \*  $p < 0.05$  ; \*\*  $p < 0.01$  ; \*\*\*  $p < 0.001$ , ns ; non significant.

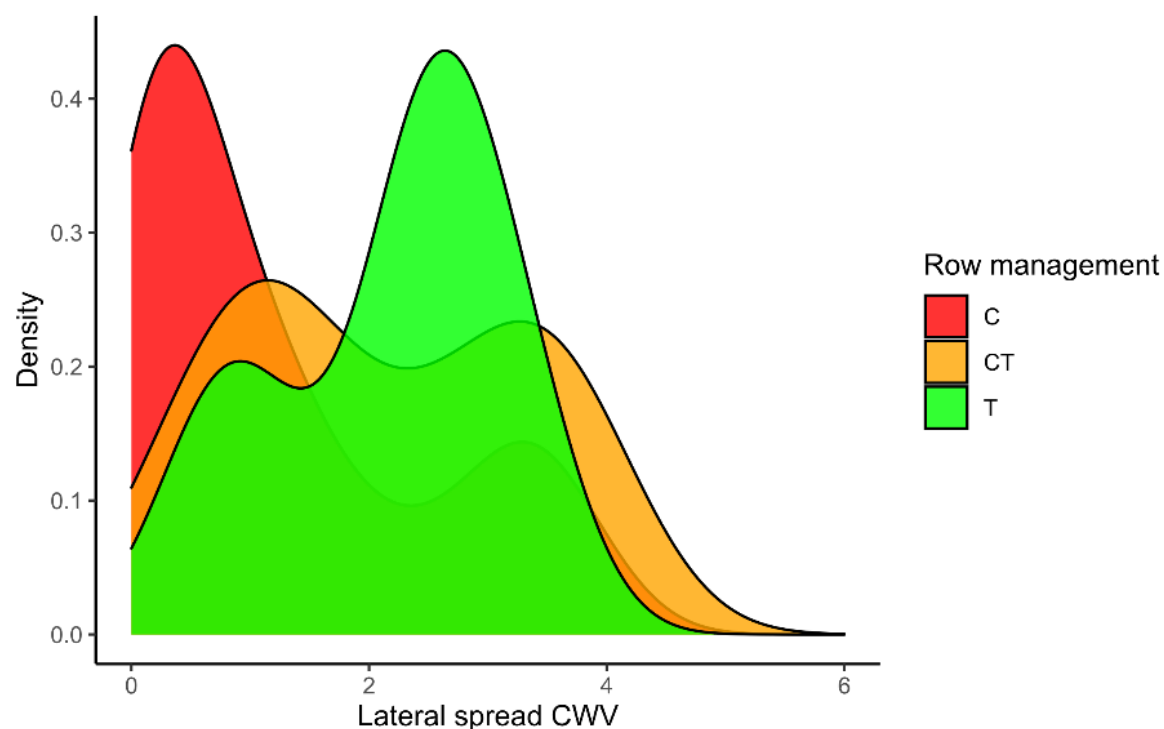




**Fig. A.16** Effect sizes of Community Weighted Variance (CWV) along the first two axes of the weed management practices and temporal variables PCA (Figure 4) in Rhône. The effect size of lateral spread CWV, flowering onset CWV and flowering duration CWV of weed community are displayed along the first PCA axis (a, c, e) and along the second PCA axis (b, d, f) respectively. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates,) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). Each point is a weed community. The color of each point specify the weed management of inter-rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; CM, combination of chemical weeding and mowing ; M, mowing ; T, Tillage). The shape indicate the weed management of rows (C, chemical weeding ; CT, combination of chemical weeding and tillage ; T, Tillage). The results of the two-tailed Wilcoxon signed-ranks test (*W*) is specified. High and low ES values quantify respectively divergent and convergent functional structure of weed communities. Significance of Wilcoxon tests are referred as following: \*  $p < 0.05$  ; \*\*  $p < 0.01$  ; \*\*\*  $p < 0.001$ , ns ; non significant.



**Fig. A.17** Densities of lateral spread community weighted variance in Languedoc from different rows managements (C, chemical weeding ; CT, combination of chemical weeding and tillage ; T, tillage).



### References in supplementary material

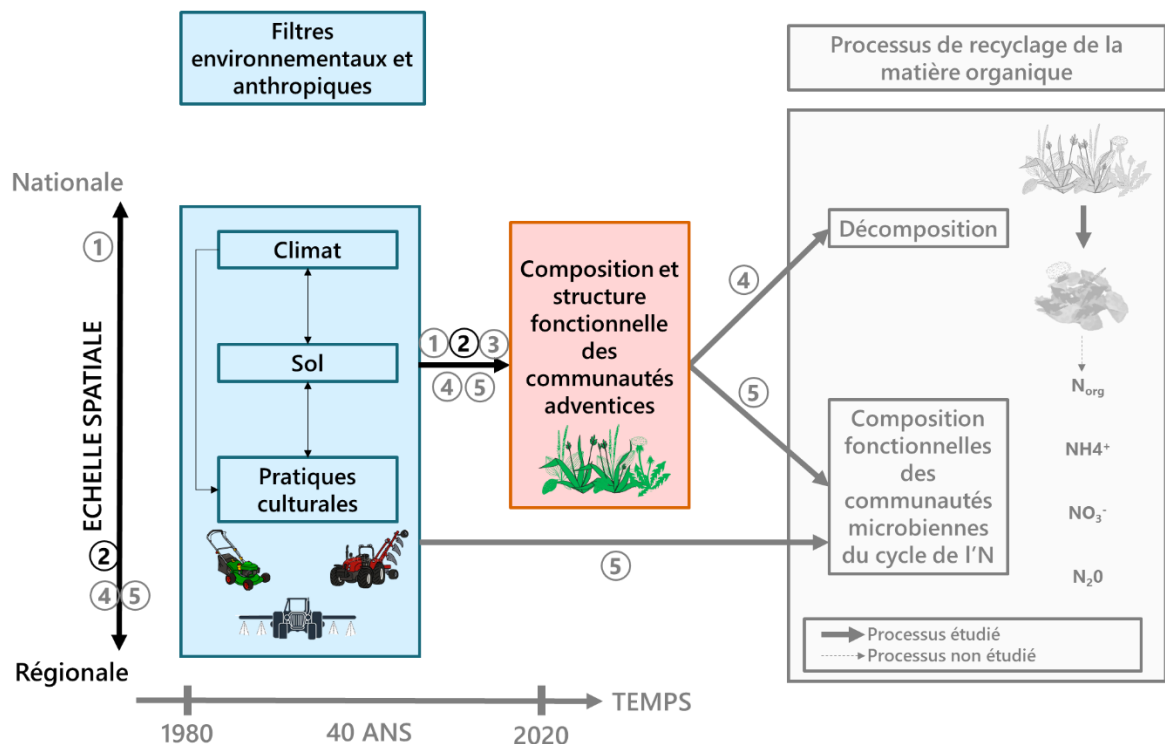
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## Chapitre 2 – Consistent response of weeds according to Grime's CSR strategies along disturbance and resource gradients in Bordeaux vineyards

Fried, G., Blanchet, C., Cazenave, L., Bopp, M., Kazakou, E., Metay, A., Christen, M., Alard, D., Cordeau, S., 2022. Consistent response of weeds according to Grime's CSR strategies along disturbance and resource gradients in Bordeaux vineyards. *Weed Res.* <https://doi.org/10.1111/wre.12549>





## **Présentation du chapitre**

Dans ce chapitre, nous passons de l'échelle nationale à l'échelle régionale du Bordelais. Ce chapitre est basé sur un jeu de données de relevés floristiques (n=400) issu d'un réseau de 100 parcelles viticoles. Ce chapitre n'est pas à formellement inclus dans le cadre de la thèse mais ces résultats nous semblaient importants à inclure dans le manuscrit de thèse pour étayer la discussion générale. **L'objectif de cette étude est d'étudier la variation des valeurs de traits de réponse et les stratégies CSR des communautés adventices le long de gradients environnementaux (de pratiques et de caractéristiques de sol). Les hypothèses de cette étude sont:**

- (i) Les conditions édaphiques déterminent la majeure partie des variations fonctionnelles des communautés adventices tandis que les pratiques de gestion n'en expliquent qu'une minorité,
- (ii) Le travail du sol et le désherbage chimique favorisent des communautés adventices rudérales tandis que la tonte favorise des communautés adventices compétitives.

Les gradients agro-environnementaux des vignobles du Bordelais s'articulent en deux axes indépendants: un axe de pratiques de gestion qui décrit l'opposition entre les vignobles tondu et travaillés et un axe de conditions édaphiques déterminé par le pH, la texture et la matière organique des sols (Figure 19). La tonte favorise les adventices hémicryptophytes à stratégie compétitive tandis que le travail du sol favorise les thérophytes, les espèces nitrophiles, et les espèces à stratégie rudérale. Les vignes sur sol acide, sableux, à faible teneur en matière organique favorisent les espèces annuelles à faible masse de graines et les adventices à stratégie stress-tolérante tandis que les vignes des sols calcaires et plus riches en matière organique favorisent les espèces pérennes, compétitives et nitrophiles avec des masses de graines élevées (Figure 19).

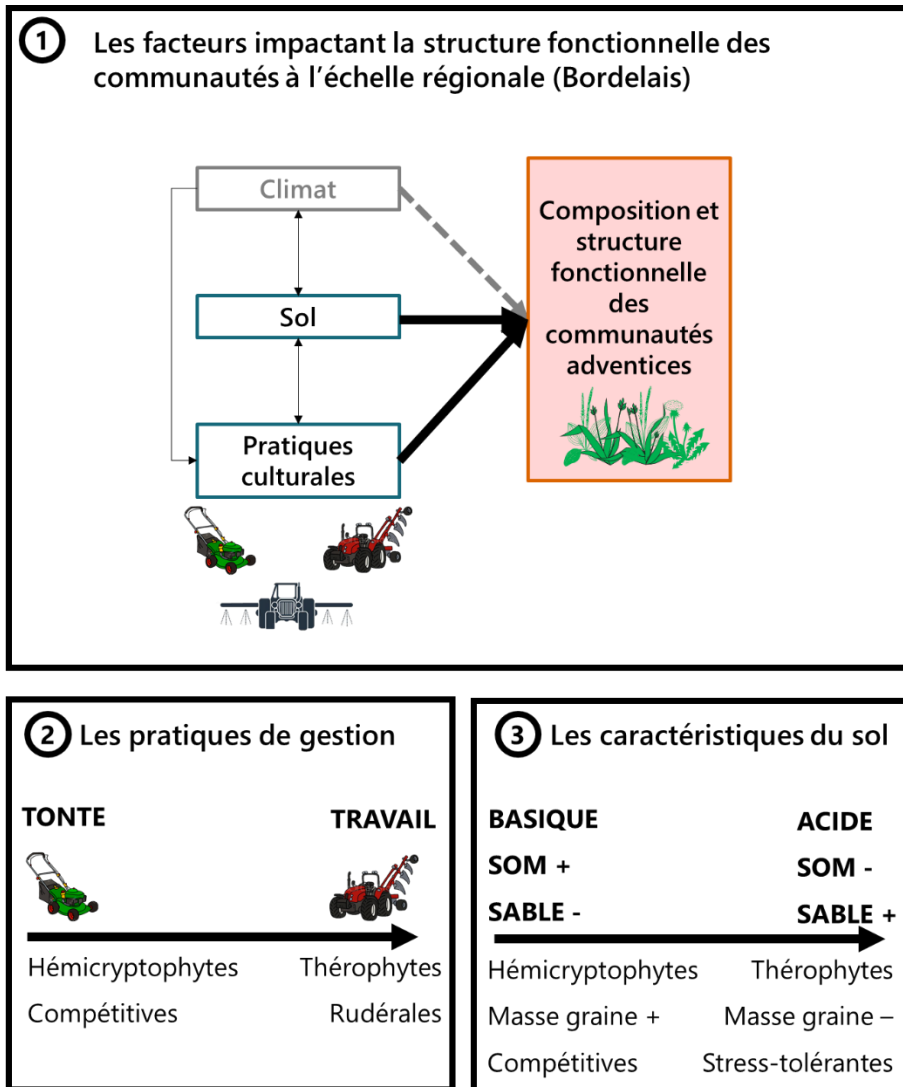


Figure 19 Résumé graphique du chapitre 2. (1) A l'échelle régionale (Bordelais), ce sont les caractéristiques du sol et les pratiques culturales qui expliquent le plus de variation fonctionnelle des communautés adventices. Les gradients agro-environnementaux des vignobles du Bordelais s'articulent en deux axes indépendants: un axe de pratiques de gestion qui décrit l'opposition entre les vignobles tondues et travaillés et un axe de conditions édaphiques déterminé par le pH, la texture et la matière organique des sols. (2) La tonte favorise les hémicryptophytes à stratégie compétitive tandis que le travail du sol favorise les thérophytes, les espèces nitrophiles et les espèces à stratégie rudérale. (3) Les vignes sur sol acide, sableux, à faible teneur en matière organique favorisent les espèces annuelles à faible masse de graines et à stratégie stress-tolérante tandis que les vignes des sols calcaires et plus riches en matière organique favorisent les espèces pérennes, compétitives et nitrophiles avec de grosses graines.

# Consistent response of weeds according to Grime's CSR strategies along disturbance and resource gradients in Bordeaux vineyards

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## Abstract

Vineyards are an appropriate model for testing the filtering effect of management practices on weed communities, as a wide range of practices (tillage, herbicides and mowing) is implemented. The aim of this study is to highlight which trait values are selected by each practice in different environmental conditions, with special references to Grime's CSR strategies. A combination of a multivariate analysis (RLQ) and the fourth-corner analysis was used to analyse 400 floristic samples belonging to 100 vineyards in the wine-growing region of Bordeaux (France). The main structure of vineyard weed communities was shaped by the opposition between mowing, favouring hemicryptophytes with a competitive strategy, and soil tillage, favouring therophytes and nutrient-demanding species with a ruderal strategy. Secondly, the vineyard weed communities differed according to the trophic status of the soil. Vineyards on acidic, sandy soils with low organic matter were characterised by small-seeded annuals with a stress-tolerant strategy whereas vineyards with clayey, calcareous soils rich in organic matter, harboured larger perennial nitrophilous species with large seeds and a competitive strategy. Our study is the first to show that weed species responded consistently to two independent gradients with specific traits associated with disturbance (life cycle and SLA) and soil resources (plant height and seed mass) gradients. Based on knowledge of the soil characteristics, it becomes possible to predict which type of weeds will develop according to the combination of practices applied on the vineyard rows and inter-rows.

## KEYWORDS

functional ecology, herbicides, management practices, mowing, response traits, tillage, vine, weed communities



## 1 | INTRODUCTION

Since Booth and Swanton's seminal article (Booth & Swanton, 2002), there have been a large number of research studies using a trait-based approach that aimed to identify general rules explaining the effect of agricultural practices on arable weed communities (Fried et al., 2009b; Gunton et al., 2011; Ryan et al., 2010; Trichard et al., 2013). In this framework, agricultural practices are considered as filters that reduce the probability of presence of species that do not have suitable trait values, progressively replaced by more adapted weed species (Booth & Swanton, 2002; Fried et al., 2009b). Weed community responses to particular practices, such as tillage, have been examined mostly in annual crops (Armengot et al., 2016; Plaza et al., 2015; Zanin et al., 1997). No-till systems have been shown to favour weed communities with more perennial plants, small plants with great affinity for nutrient-rich soils, flowering later in season and producing a high number of small seeds compared to those observed in conventional tillage systems (Armengot et al., 2016). From a functional point of view, the effect of herbicides on weed communities has been less studied, although it was shown that herbicides selected for late-emerging weed species whose life cycle avoid the herbicide filter (Fried et al., 2012; Gulden et al., 2010). The effect of fertilisation has been even less investigated (but see Cordeau et al. (2021)) even if diachronic studies suggested indirectly that increased amount of N-fertilisation can favour nitrophilous weeds (Fried et al., 2009a).

Highlighting the role of management practices on the assembly of weed species into communities is challenged by the interaction between practices coherently implemented by farmers, and the interaction between practices and the environmental abiotic conditions (e.g., the effect of fertilisation can be hindered by the effect of the natural soil fertility). One option is to experiment and control for different factors in experimental farms (see e.g., Ryan et al. [2010]). However, even if a trait-based approach sheds light on filtering mechanisms, conclusions of experiments remain strongly limited to local conditions (e.g., soil type, weather and species pool). To overcome these limitations, the analysis of large-scale weed surveys covering wide gradients of disturbance (generated by farming practices) and environmental factors (available resources and climate) is required. Indeed, Gaba et al. (2014) suggested that the effects of cropping systems on the environment can be summarised into disturbance and resource gradients with distinct plant traits responding to each component of the two gradients. According to Grime's CSR strategies (Grime, 1974, 1977; Pierce et al., 2017), distinct plant strategies should be observed along these two gradients with competitive species (C) in the more productive and less disturbed fields, ruderal species (R) in the more disturbed fields and stress-tolerant (S) in the less productive and less disturbed fields. So far, even if the application of CSR strategies has largely been used for managed grasslands (Moog et al., 2005), few studies have tested if these strategies responded to agricultural disturbance and resource gradient in vineyards.

The response of weed communities to farming practices through a functional approach has been extensively studied in annual field crops (for a review, see Gaba et al. [2017]). However, weeds and crops grow in fertile environments and weeds are often managed with

herbicides, reducing the length of disturbance and resource gradients explored. Conversely, the grapevine is a more relevant and understudied system for analysing the link between agricultural practices and weed trait values. First, at the regional scale, management practices in vineyards are very diversified (including combinations of tillage, mowing and herbicides) and vines are planted in a very varied context of soil resources (including on dry hillsides or on poor sandy or stony soils), generating larger gradients than annual crop fields both in terms of disturbance and resources. Second, at the vineyard scale, distinct management practices are usually applied on the rows and inter-rows of the crop. For example, in an increasing number of vine regions, the inter-rows are mowed or tilled while only the rows are sprayed with herbicides. Additionally, as vineyards are permanent crops, practices are less likely to change from year to year as in traditional crop rotation, thus allowing patterns to emerge (i.e., correlation between species and practices).

Previous studies on weed communities in vineyards have shown that management practices can influence weed community composition and diversity (Fried et al., 2019; Gago et al., 2007; Lososová et al., 2003). Weed diversity and abundance generally decrease as tillage or herbicide use increases, while mowing leads to richer communities with more abundant species (Fried et al., 2019; Kazakou et al., 2016). Different management practices (tillage vs. herbicides) also lead to particular species assemblages, suggesting a different filtering effect (Fried et al., 2019). From these taxonomic studies, it was already established that annuals are generally favoured in tilled/sprayed vineyards, while mowing allows the survival of perennials. However, due to the high diversity of species found in vineyards (e.g., around 900 species in France [Maillet, 2006]), taxonomic approaches have failed to highlight consistent responses of weeds to management practices. More recently, an increasing number of studies have investigated the response of weed communities to vineyard management, using a trait-based approach (Bopp et al., 2022; Guerra et al., 2021; Hall et al., 2020; Kazakou et al., 2016; MacLaren et al., 2019; Mainardis et al., 2020). MacLaren et al. (2019) showed that herbicide-treated sites promoted relatively tall, small-seeded weeds, indicators of a ruderal-competitive life strategy. Kazakou et al. (2016) and MacLaren et al. (2019) highlighted that tillage favoured ruderal species with high SLA (specific leaf area). However, the effect of mowings showed contrasted results, promoting either shorter (MacLaren et al., 2019) or taller weeds (Bopp et al., 2022; Kazakou et al., 2016; Mainardis et al., 2020), so lacking a totally clear signal on the selected Grime strategy. One possible reason for these mixed results regarding Grime strategies is that these studies either considered only the inter-rows (Hall et al., 2020; Kazakou et al., 2016), only the rows (Mainardis et al., 2020) or used samples that indistinctly cover the vegetation over both rows and inter-rows (MacLaren et al., 2019). As management practices can be very contrasting between the inter-rows and the rows (typically, herbicides sprayed on the rows, mowing in the inter-rows), distinct weed surveys on these two areas may allow to disentangle more easily the effect of the environment (climate and soil) from the effects of the practices. Another limitation of these studies is that they do not explicitly take into account the resource gradient, except for Guerra et al. (2021) who

show that irrigation favours taller and more competitive species. We expected that tillage and herbicide would favour ruderal communities while mowing would select more perennial communities. Indeed, tilled and sprayed vineyards both experience disturbance of high intensity that destroy all the vegetation biomass while mowing removes it partially. Taking into account the soil richness gradient and fertilisation, we also hypothesise that regardless of management practices, vineyards on fertile and/or fertilised soils will favour competitive species and vines with poor resources (sandy texture and low organic matter) and/or low fertilisation will favour stress-tolerant species.

Additionally, landscape data can help understand how the land cover around the studied vineyards influences weed community composition or diversity in the vineyards (Hall et al., 2020). Many studies have examined local plant diversity as a function of habitat-specific communities in a mosaic landscape (Honnay et al., 2003; Wagner et al., 2000) and some supported the hypothesis that local plant species richness in arable fields is influenced by processes operating at the landscape scale (Gabriel et al., 2005). However, much fewer studies have considered the landscape filtering effects on traits, for example, on dispersal which is a major landscape-level ecological process (Duflot et al., 2014).

The objective of the study is: (1) to characterise the agro-environmental gradient of the vineyards (in a disturbance and resource gradient), (2) to identify the response trait values of the species along these two gradients and (3) to test if the Grime's CSR strategies of the species are selected by the resource and disturbance gradients. In accordance with the literature discussed above, we hypothesised that distinct management practices will select specific functional types of weeds (those possessing the requisite trait values to pass through the filters) and that Grime's CSR strategies can summarise these along the disturbance and the resource gradients.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and vegetation surveys

Plant communities, management practices and environmental variables were surveyed in the Bordeaux wine-growing region (South-West of France), one of the world's most famous wine regions although the second in size after the Languedoc wine region. Floristic surveys were performed during spring and summer 2015 in 100 vineyards mostly distributed in the Gironde department (Figure 1A,B). In each vineyard surveyed, the sampling area covered two distinct rows and four distinct inter-rows (Figure 1Cs). For each of these six plots, sampling consisted in the identification of the flora (presence and abundance of species) over a length of 25 m and a width of 1 m, which corresponded to a total of 150 m<sup>2</sup> per vineyard (Figure 1C). Abundance was estimated based on the cover percentage of each species per plot. The sampled rows (R) and the inter-rows (IR) of each vineyard were randomly chosen. Potential edge effects were avoided by locating the surveyed area beyond two stakes from the edge (i.e., around 10 m). In each area, vegetation was recorded twice: first at the end of March/beginning of April,

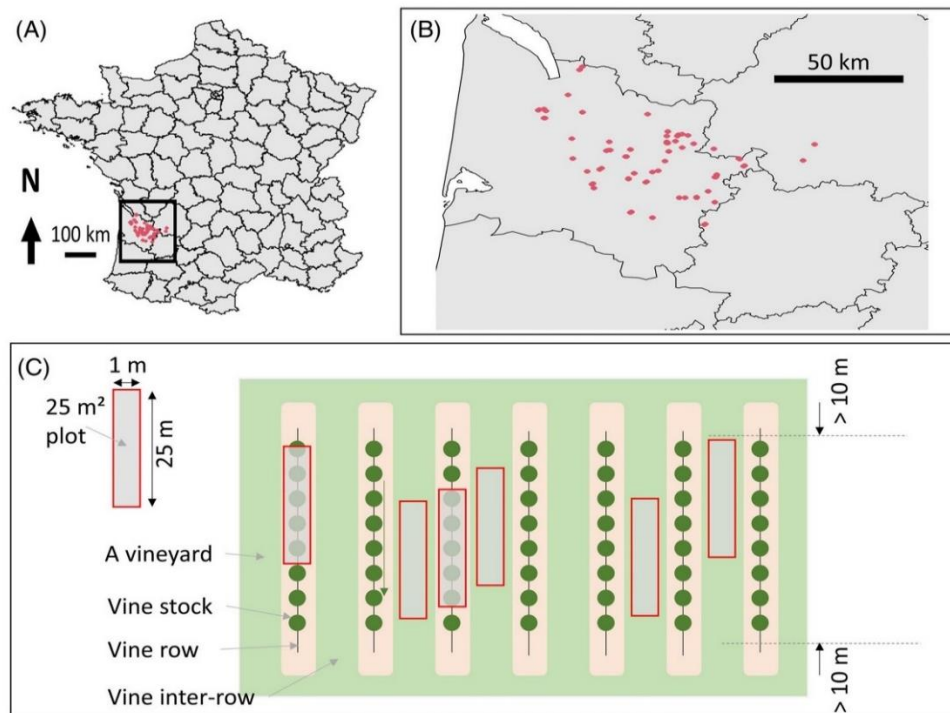
that is, before the first vegetation management (i.e., herbicides, tillage and mowing) were applied in the vineyard; second, at the end of June/beginning of July, that is, after all management practices have been applied. We performed 400 vegetation surveys describing vegetation in the rows in spring (100 samples) and in summer (100 samples) as well as vegetation in the inter-rows in spring (100 samples) and in summer (100 samples).

### 2.2 | Environmental variables and management practices

Climatic conditions were summarised by the annual mean temperature, mean rainfall and mean potential evapotranspiration of the year 2015 based on the data of the TRYDEA tool (French Institute of Wine and Vineyards, Table 1). Soil was sampled at two depths: 0–30 and 30–60 cm, using an auger. On each vineyard, six auger samples were taken on two inter-rows of the vineyards and six others on two rows of the vineyards in the same area where the vegetation was surveyed. The samples were pooled to have one soil analysis per surveyed vineyard. The analyses were performed by the AUREA laboratory based in Blanquefort (Gironde, France) and included: Clay/Silt/Sand percentages, Calcareous content, Organic matter content, Carbon/Nitrogen ratio, pH measured with water, pH measured with KCl, Cation exchange capacity, P<sub>2</sub>O<sub>5</sub> content, K<sub>2</sub>O content, MgO content. As several soil variables were correlated, we performed a Principal Component Analysis (PCA) and kept the first three axes, which represented 66% of the inertia and represented the percentage of sand (PCA axis 1), organic matter content (PCA axis 2) and Calcium carbonate content (CaCO<sub>3</sub>) (see Figure S1). We considered that the soil nutrient gradient is positively related to organic matter content and negatively related to sandy texture.

The landscape database had been obtained in a previous study (Boisson, 2016) that characterised the landscape in a 100 m buffer zone around the vineyard with the proportion and the area of each land cover type (urban zones, annual crops, perennial crops, bodies of water, grasslands, vineyards, forests and woodlands, as well as a miscellaneous category). After performing a PCA on all the 19 landscape variables (not shown), we decided to summarise landscape metrics by the percentage of vineyard area in the buffer zone (negatively correlated with the Shannon diversity index of land cover types). This variable represented the homogeneity of the landscape surrounding the studied vineyards (i.e., low values mean high heterogeneity of the landscapes with hedges, grasslands and other types of land uses, while high values mean mainly other vineyards around the studied vineyards).

The management practices applied in the vineyards were collected through an interview of the winegrowers involved. Management practices were summarised by the number of soil tillage in the rows (till\_r) and inter-rows (till\_ir), the number of mowings in the rows (mow\_r) and the inter-rows (mow\_ir), and the number of herbicide treatments (applied at the recommended dose), the latter always being applied in the rows only (herbi\_r). The number of applications of fertiliser (chemical or organic) and the total number of tractor passes



**FIGURE 1** Location of the sampled vineyards (red dots,  $N = 100$ ) (A) in Southwestern France and (B) in the Gironde department. (C) Illustration of the sampling protocol per vineyard.

(including fungicide treatments, harvesting, etc.) were also included. This latter variable is the sum of the number of tractor passes which is an indirect measurement of soil compaction. In 2016, the dominant model of management practices in the Bordeaux wine region corresponded to chemical weed control in the rows (1.8 treatments on average), coupled with mechanical weed control in the inter-rows with an average of 1.9 tillage operations and 2.1 mowing (based on Simionici [2019], see Table 1 for comparison with the studied network). Vegetation cover in the inter-row was present in 84% of Bordeaux vineyards (92% in our network). Most of the time, it was a permanent cover of spontaneous vegetation (75%), more rarely a permanent (6%) or temporary (3%) sown cover crop. Organic farming was implemented in 11.6% of the Bordeaux vineyards (compared to 40% in our network). Table 1 gives the range (min/max), mean values and standard deviation of all environmental, landscape and management variables. This indicates the assumed link between traits and variables plus disturbance and resource gradients.

### 2.3 | Plant traits and Grime's CSR strategies

Five traits were selected and summarised in Table 1. Maximum plant height at maturity represents the ability to compete for light with neighbouring plants (Westoby et al., 2002). SLA represents the ability to acquire and use resources during the favourable period, and is

positively correlated to the relative growth rate of weed seedlings (Storkey, 2004). Flowering phenology (onset and period) is a key trait in disturbed habitats (Gaba et al., 2017). An early flowering period is usually associated with fast-growing and small-statured species. These early emerging species, with early flowering onset and short life cycle, are expected to better escape management practices, because they can produce seeds before the first vegetation management occurring at the end of March (Gaba et al., 2017). High seed production (often associated with low seed mass) can indicate a greater seed bank and counterbalance high mortality rates due to herbicide applications (Storkey et al., 2010). In addition to these five traits, we also used Raunkiaer's life forms assuming that therophytes and geophytes are more adapted to disturbance than hemicryptophytes and woody species. Finally, the Ellenberg indicator value for nitrogen (Ellenberg-N) was considered as a synthetic nutrient requirement trait. Increasing rates of fertilisation in arable fields have been shown to favour nitrogen-demanding species (Cordeau et al., 2021; Fried et al., 2009a, 2009b). In the following analyses, plant height and seed mass were log-transformed to ensure normality.

In addition, we also used Grime's classification of plants in the CSR strategies (Grime, 1977; Hodgson et al., 1999) as a supplementary grouping of species (not influencing the analysis). Our list of 200 species fall into seven categories: C (35 species), S (7 species), R (58 species), CR (32 species), CS (8 species), SR (15 species) and CSR (40 species). Five species were not assigned to any group.

**TABLE 1** List of environmental variables (climate and soil characteristics), management practices and selected traits with their abbreviations, units, basic statistics and their coordinates on the first two RLQ axes of the global analysis. For the soil variables, the means, standard deviation and ranges refer to the main variables influencing the PCA axes (more informative than the values of the PCA coordinates). The disturbance and resource gradient column gives the expected relationships (–: Negative, +: Positive) of variables and traits with these two gradients

Climate, soil, management practices and traits, and unit	Abbreviation	Disturbance (D) and resource (R) gradient	Mean $\pm$ SD or number	Range (min–Max)	RLQ axis 1	RLQ axis 2	Sources
Temperature ( $^{\circ}$ C)		R (+)	12.5 $\pm$ 1.2	10.3–14.1	0.07	–0.17	TRYDEA
Rainfall (mm)		R (+)	675 $\pm$ 47	594–849	0.08	–0.03	TRYDEA
PCA Soil Axis 1 Sand (%)	Sand	R (–)	47.8 $\pm$ 23.5	3–87.2	0.28	0.72	Soil analysis
PCA Soil Axis 2 Organic matter	Org mat	R (+)	1.8 $\pm$ 0.8	0.4–4.6	0.08	–0.34	Soil analysis
PCA Soil Axis 3 [CaCO <sub>3</sub> ]	Calc	R (+)	34.2 $\pm$ 71.6	0–271	0.27	–0.49	Soil analysis
Percentage of vineyard	V_100m		77.3 $\pm$ 17.3	29.4–100	0.08	–0.08	Boisson (2016)
No. of mineral fertilisation in the last 5 years	feng	R (+)	2.1 $\pm$ 2.1	0–5	–0.04	0.14	Interview with farmers
No. of organic fertilisation in the last 5 years	famo	R (+)	6.5 $\pm$ 2.4	0–13	0.15	0.08	Interview with farmers
No. of herbicide treatments	nherb	D (+)	0.9 $\pm$ 1.1	0–3	–0.10	0.13	Interview with farmers
No. of tillage on the inter-rows (till <sub>ir</sub> )	till <sub>ir</sub>	D (+)	1.8 $\pm$ 1.7	0–8	0.58	0.04	Interview with farmers
No. of tillage on the rows	till <sub>r</sub>	D (+)	2.2 $\pm$ 2.4	0–8	0.45	–0.01	Interview with farmers
No. of mowings on the inter-rows	mow <sub>ir</sub>	D (–)	3.5 $\pm$ 1.8	0–7	–0.29	0.08	Interview with farmers
No. of mowings on the rows	Mow <sub>r</sub>	D (–)	0.6 $\pm$ 1.4	0–5	–0.21	–0.14	Interview with farmers
Total number of mechanical passes	npm	D (+)	26.7 $\pm$ 5.4	15–40	0.35	–0.12	Interview with farmers
<b>Raunkiaer life forms</b>							baseflor (Julve, 1998)
Therophytes	Thero	D (+)	<i>n</i> = 98	–	0.85	0.07	
Biennials	Bis		<i>n</i> = 9	–	0.21	–0.49	
Geophytes	Geo	D (+)/R (+)	<i>n</i> = 23	–	0.17	–0.44	
Hemicryptophytes	Hemi	R (+)	<i>n</i> = 64	–	–1.16	0.12	
Woody species	Woody		<i>n</i> = 6	–	–1.43	–0.50	
Specific leaf area (m <sup>2</sup> kg <sup>–1</sup> )	SLA	D (+)	25.49 $\pm$ 7.21	5.55–53.24	0.15	–0.03	LEDA
Maximum plant height (m)	Height	R (+)	0.91 $\pm$ 2.11	0.1–30	–0.16	–0.48	Flora Gallica
Seed mass (g)		R (+)/D (–)	3.04 $\pm$ 10.18	0.0095–120	–0.01	–0.67	SID
Month of flowering onset (months)	Flow. On.	D (–)	4.20 $\pm$ 1.57	1–8	–0.28	–0.10	baseflor (Julve, 1998)
Flowering period (months)	Flow. Per.	D (+)	5.13 $\pm$ 2.23	2–12	–0.03	0.04	baseflor (Julve, 1998)
Ellenberg indicator value for nutrient	EIV-N	R (+)/D (+)	5.78 $\pm$ 1.59	1–9	0.16	–0.52	baseflor (Julve, 1998)

## 2.4 | Data analysis

To identify significant relationships between the plant traits in vineyards and the environmental and management variables, we followed the framework developed by Dray et al. (2014) combining the RLQ multivariate technique (an ordination analysis) and the fourth-corner analysis (a hypothesis testing analysis). Contrary to classical unconstrained ordination analyses such as DCA or NMDS, RLQ is a constrained ordination in which the scores of both rows (samples) and columns (species) are constrained by linear combinations of predictor variables (i.e., environmental variables and traits). RLQ assigns scores to species, sites, traits and environmental variables along orthogonal axes and provides a graphical summary of the main data structures (Dolédéc et al., 1996), while the fourth-corner analysis tests for associations between one trait and one environmental variable at a time

(Dray & Legendre, 2008). While the RLQ analysis does not allow identifying precisely which environmental variable acts on which trait, the fourth-corner analysis does not account for the covariation among traits or among environmental variables. The two approaches are therefore complementary.

In the main analysis, we performed RLQ, fourth-corner analysis and their combination at the scale of the 100 vineyards, merging the four samples available (rows and inter-rows, spring and summer) by using the highest abundance scores of a species in one of the four samples. Second, to detect trait-environment relationships that may only exist in certain situations, we performed a fourth-corner analysis separately on the samples of the rows (200 samples) and inter-rows (200 samples) for both seasons, including the period of observation (spring versus summer) as an explaining variable. Similarly, we analysed separately the samples of spring (200 samples) and summer

(200 samples), including the variable area, distinguishing the row and the inter-row, as an explaining variable. In the following, these subsets of the data set will be referred to collectively as subsets, or row subset, inter-row subset, spring subset or summer subset.

Both RLQ and the fourth-corner analysis use three tables: the R-table, which consists of the 100 (or 200 for the subsets) samples described by the 15 agro-environmental (and one seasonal variable (spring vs. summer) for the row and inter-row subsets and a spatial variable (row vs. inter-row) for the spring and summer subsets), the Q-table containing the 200 species described by their seven features (five traits, Raunkiaer's life forms and Ellenberg-N) and the L-table describing the floristic composition of the 100 (or 200) samples via the abundance of the 200 species. The L-table therefore is linked with the R- and the Q-tables in the analysis through common identifiers of samples or species. RLQ selects the axes that maximise the co-variance between the site scores constrained by the agro-environmental variables (the R-table) and the species scores constrained by the species traits (the Q-table). A Monte-Carlo permutation ( $n = 999$ ) test was used to test the null hypothesis ( $H_0$ ) of absence of link between the agro-environmental Table (R) and the trait Table (Q).

Thereafter, the fourth-corner statistic (Dray & Legendre, 2008) was used to test the significance of the direct trait-environment relationships on these 100 (200) samples. This method measures the link between species traits and environmental variables using either (1) a Pearson correlation coefficient  $r$  for two quantitative variables, (2) a Pearson Chi-square ( $\chi^2$ ) and G-statistic for two qualitative variables or (3) pseudo-F and a Pearson correlation coefficient  $r$  for one quantitative and one qualitative variable. A permutation model was applied to test the null hypothesis ( $H_0$ ) that species are distributed independently of their preferences for environmental conditions and of their traits (using the permutation model 6 of Dray et al., 2014). We performed 49 999 permutations and used the false discovery rate method (Benjamini & Hochberg, 1995) to adjust  $p$  values for multiple testing. In the final step, we combined the two analyses by applying the fourth-corner tests directly on the outputs of RLQ analysis. This latter approach consists in testing the associations between individual traits and environmental gradients obtained from RLQ scores, and between individual environmental variables and trait syndromes obtained from RLQ scores (Dray et al., 2014).

The Grime's CSR strategies of species were also projected as supplementary individuals on the first (global) RLQ axes to assess the consistent response of these strategies on the highlighted trait-environment gradients. Significant differences between the distribution of Grime's CSR strategies on the RLQ axes were tested by a Kruskal-Wallis test followed by multiple pairwise comparisons with the Dunn test. All the statistics were run with R (Team RC, 2020) and the ade4 package (Dray & Dufour, 2007).

### 3 | RESULTS

A total of 200 plant species were observed across the 100 vineyards. Nine species were present in more than 90% of the vineyards: *Taraxacum officinale* (100 vineyards), *Sonchus asper* (99), *Poa annua* (97),

*Senecio vulgaris* (96), *Convolvulus arvensis* (95), *Veronica persica* (94), *Plantago lanceolata* (94), *Cerastium glomeratum* (91) and *Trifolium repens* (90).

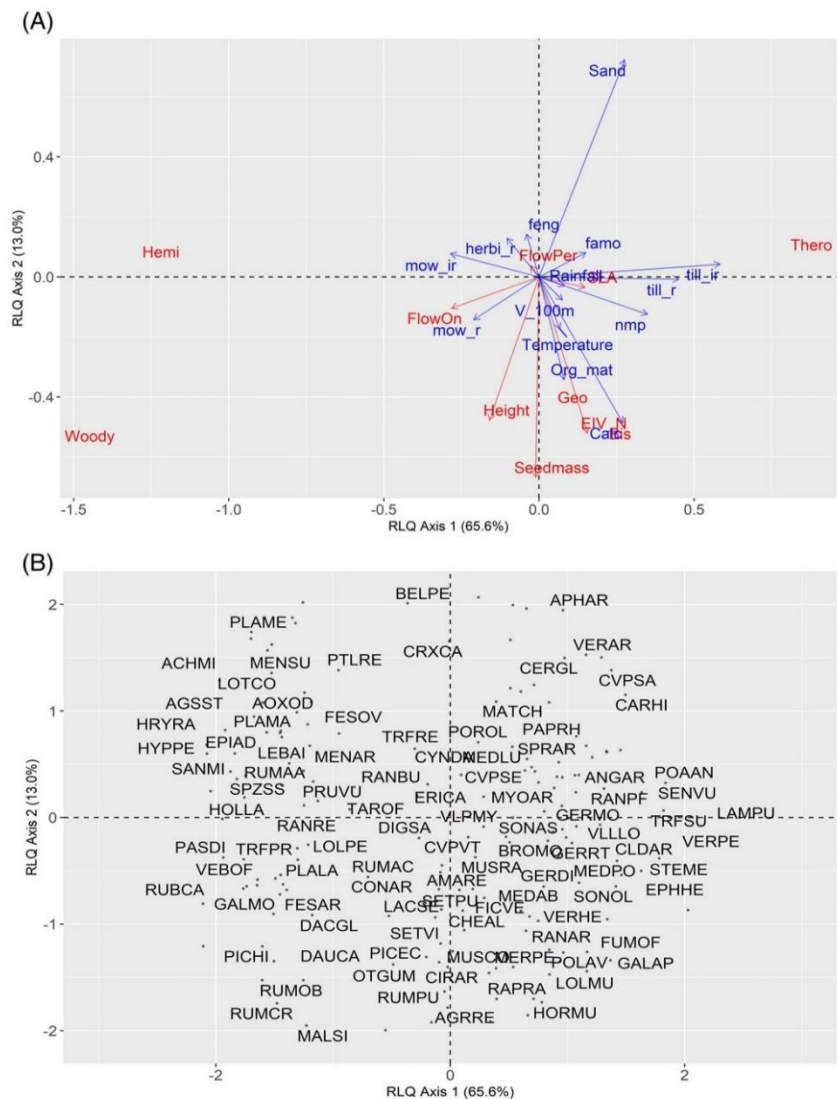
#### 3.1 | Global responses of weed communities at the vineyard scale

The first two axes of the RLQ accounted for 78.6% of the total inertia. Environment significantly influenced the distribution of species based on their trait values (Model 2,  $p < 0.001$ ,  $N = 999$  permutations of the samples) and traits significantly influenced species assemblages found in samples with given environmental conditions (Model 4,  $p < 0.001$ ,  $N = 999$  permutations of the species). RLQ axis 1 (65.6%) discriminated primarily the management practices along a disturbance gradient, while RLQ axis 2 (13.0%) was related to abiotic factors along a soil resource gradient (Figure 2A). There was a slight correlation between the amount of mineral fertilisation and RLQ axis 2 (sand content), indicating that vinegrowers with poorer soils apply more fertiliser, but fertilisation contributed poorly to RLQ axis 2 compared to soil variables.

RLQ axis 1 was positively correlated with the number of soil tillages in the R and the IR and negatively correlated with the number of mowings both in the R and the IR (Table 1 and Figure 2A). To a lesser degree, RLQ axis 1 was also positively correlated to the total number of mechanical passages but negatively correlated to the number of herbicide treatments. Regarding species features, RLQ axis 1 discriminated Raunkiaer life forms. Hemicryptophytes, woody species and species with high maximum plant height and late flowering onset were negatively correlated to RLQ axis 1 (associated with mowing) and opposed to therophytes and species with high SLA (associated with tillage) (Table 1 and Figure 2B). RLQ axis 2 was positively correlated with sand percentage and negatively correlated with organic matter content and calcium carbonate content. RLQ axis 2 opposed vineyards with several herbicide applications and high use of mineral fertilisers in production areas with low temperatures versus vineyards with low chemical use in production areas with high temperatures (Table 1, Figure 2A). Regarding species traits, RLQ axis 2 discriminated traits related to competitive ability (seed mass, plant height and Ellenberg indicator value for nitrogen). RLQ axis 2 was negatively correlated with seed mass, Ellenberg indicator value for nutrients, geophytes and maximum plant heights, that is, these traits are positively correlated with more fertile soils (Table 1 and Figure 2B).

The fourth-corner analysis showed 18 significant correlations (over 154 possible, i.e., 12%) between environmental variables and traits (see correlation and  $p$  values in Figure 3). Hemicryptophytes were positively correlated with the number of mowings in the IR and negatively correlated with the number of soil tillages in the R and IR, with the number of mechanical passages as well as with the sand percentage and calcium carbonate. Conversely, therophytes were positively correlated with the number of soil tillages both in the R and IR and negatively correlated with the number of mowings in the R and IR. Therophytes were also positively correlated with the sand

**FIGURE 2** Results of the first two axes of the RLQ analysis: (A) coefficients for environmental variables (blue) and traits (red), (B) scores of species. Codes for variables and traits are given in Table 1. Species names are abbreviated with Eppo codes.



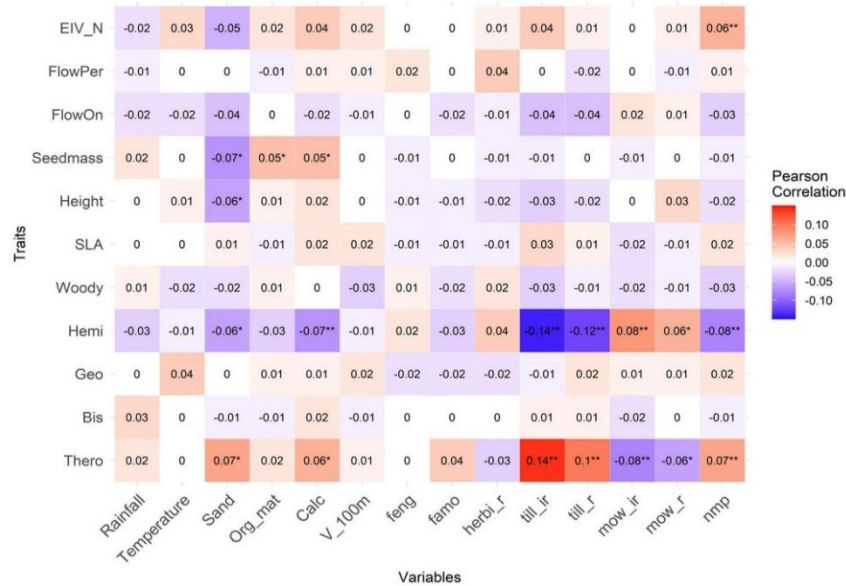
percentage and calcium carbonate content. Finally, maximum plant height and seed mass were negatively correlated with the sand percentage, and seed mass was positively correlated with calcium carbonate content and organic matter.

The combination of RLQ and fourth-corner analyses showed that early flowering annual species were positively associated with RLQ axis 1, that is, associated with soil tillage, high numbers of mechanical passages, and organic fertilisation on sandy or calcareous soils, while late flowering hemicryptophytes were negatively associated with RLQ axis 1, that is, associated with mowing (Figure 4). Species with high values of maximum height, seed mass and Ellenberg values for nitrogen were associated with RLQ axis 2, that is, positively associated with calcium carbonate content and negatively with sand percentage.

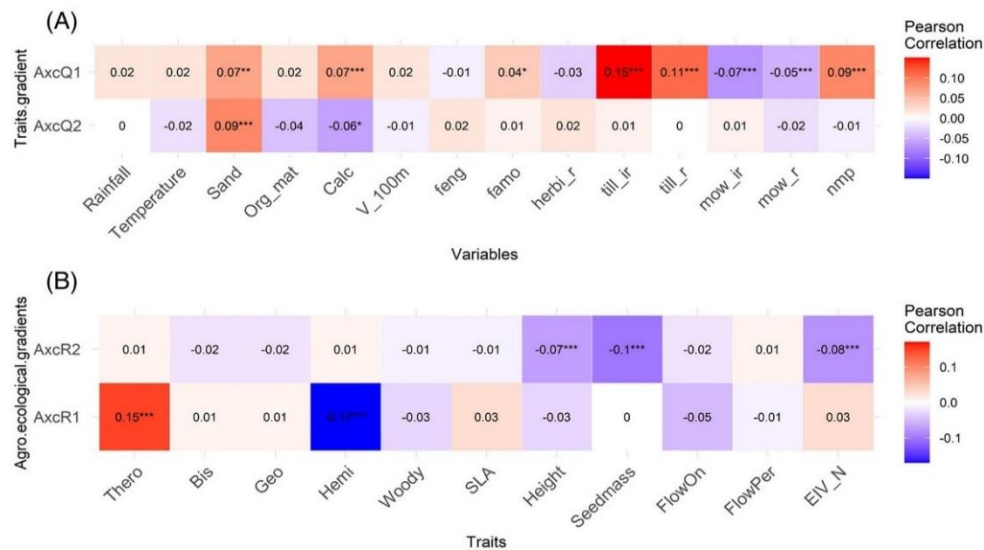
### 3.2 | Specific responses of weed communities at the scale of rows, inter-rows, spring or summer seasons

The results of the fourth-corner analyses with the row, inter-row, spring and summer subsets were largely similar to those obtained at the vineyard scale (presented above), in particular, the association of hemicryptophytes with mowing, therophytes with tillage and the positive association between seed mass, organic matter and calcium carbonate content in the soil (see Figure 5 for a summary of the results, Table S1 gives the detailed relationships for each subset).

However, some additional relationships were highlighted only at the scale of some or several of these subsets. The fourth-corner analyses in the R and the IR indicated a strong association between flowering onset



**FIGURE 3** Results of the fourth-corner tests. Positive and negative associations (Pearson's correlation  $r$ ) between environmental variables (detailed in Table 1) are in red and blue, respectively. \* $p < 0.05$ , \*\* $p < 0.01$ .



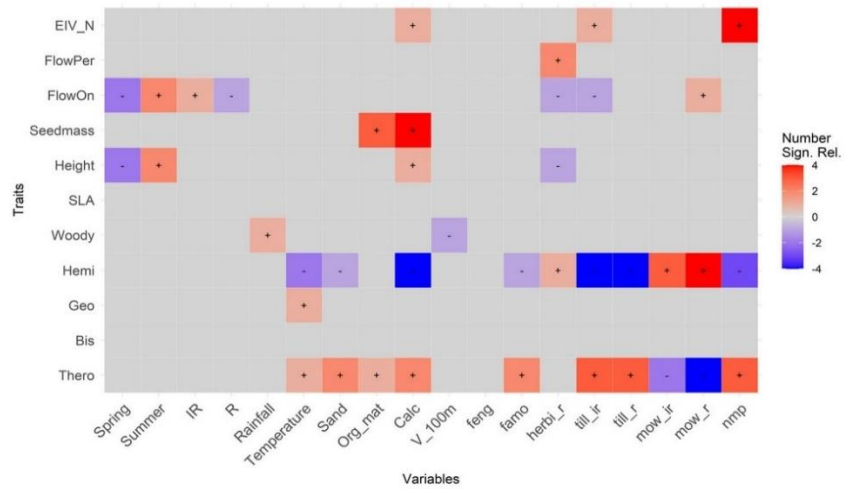
**FIGURE 4** (A) Fourth-corner tests between the first two RLQ axes (AxcQ1 and AxcQ2) for trait syndromes and environmental variables (detailed in Table 1). (B) Fourth-corner tests between the first two RLQ axes for environmental gradients (AxcR1/AxcR2) and traits (detailed in Table 1). Positive and negative associations (Pearson's correlation  $r$ ) between environmental variables (detailed in Table 1) are in red and blue, respectively. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

and sampling season and also highlighted a positive link between plant height and season, that is, taller species in summer compared to spring (Figure 5). Flowering onset was also positively related to the inter-rows (and negatively related to the rows), that is, later flowering onset in the IR.

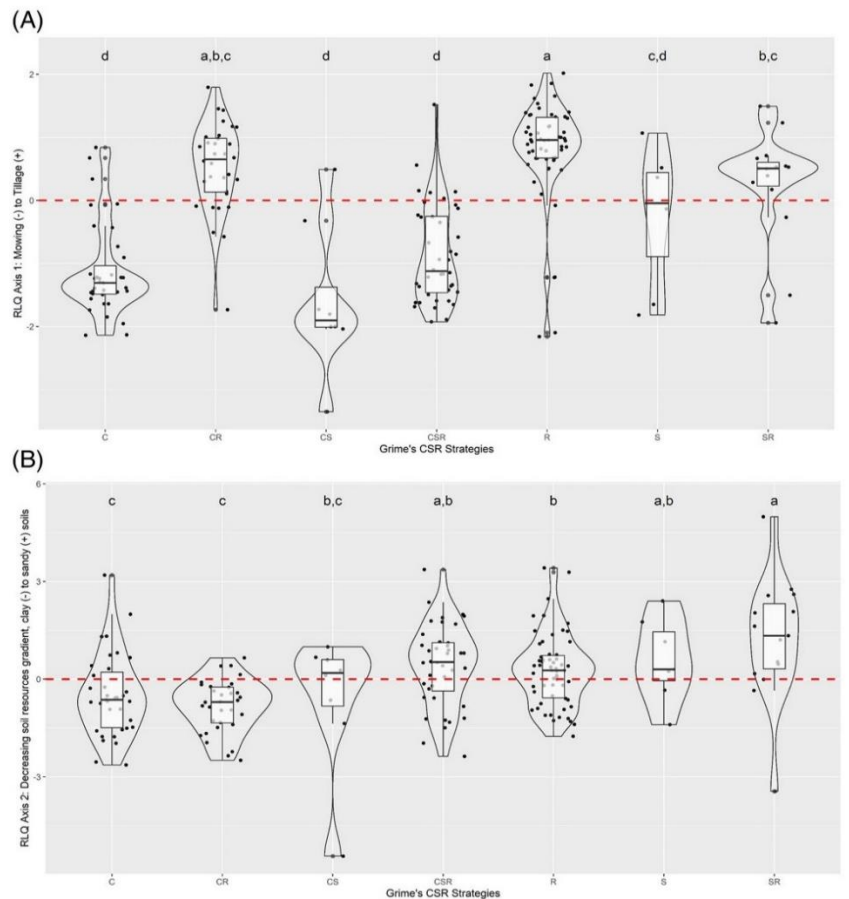
The effect of some management practices was only detected with subsets. For example, the number of herbicide applications was correlated with short early flowering species with a long flowering period when analysing the summer subset. Tillage in the IR was associated with early

flowering species (spring subset) and with species having high nutrient requirements (summer subset). Conversely, mowing on the R was related to late flowering species (spring subset). On the row dataset, the proportion of woody perennials increased with the diversity of landscape (negative relationship with percentage of vineyards in the surroundings) and with rainfall. Finally, temperature was positively related to therophytes (IR subset) and geophytes (spring subset) and negatively related to hemi-cryptophytes (R and IR subsets).

**FIGURE 5** Number of positive (+) or negative (–) significant traits × environment relationships based on the fourth-corner analysis applied on the row, inter-row, spring and summer subsets. From light to dark red, there is 1–4 significant relationships, and from pale purple to dark blue there is 1–4 significant relationships. The detailed correlation are available in Table S1.



**FIGURE 6** (A) Distribution of weed species according to their Grime's CSR strategies (as supplementary variable) on the RLQ axis 1 (positively correlated to soil disturbance by tillage) and (B) on the RLQ axis 2 (negatively correlated with the soil resource gradient). Different letters indicate significant differences ( $p < 0.05$ ) based on a Dunn test.



### 3.3 | Grime's CSR strategies in vineyards

Plotting Grime's CSR strategies as a supplementary variable on the RLQ analysis at the vineyard scale yielded in consistent results

(Figure 6). The Kruskal–Wallis test indicated significant differences in the distribution of the CSR strategies on both RLQ axis 1 (Kruskal–Wallis  $\chi^2 = 101.74$ ,  $df = 6$ ,  $p < 0.001$ ) and 2 (Kruskal–Wallis  $\chi^2 = 40.19$ ,  $df = 6$ ,  $p < 0.001$ ). RLQ axis 1, which expressed a soil



disturbance gradient, opposed ruderal strategies associated with tillage to competitive (C) strategies associated with mowing (Figure 5A). The mixed strategies CR and SR were associated with the R strategy while the CS and CSR strategies were associated with the C strategy. Finally, the stress-tolerant strategy (S) was located in the middle of the gradient. RLQ axis 2, which expressed a soil resource gradient, opposed C and CR strategies on clay soils with high organic matter and calcium carbonate content to S and SR strategies on sandy acidic soils with low organic matter. CS, CSR and R strategies were in the middle of the gradient.

## 4 | DISCUSSION

Our results highlighted a strong functional differentiation of vineyard weed communities along two orthogonal disturbance and resource gradients. Among the management practices, the opposition between tilled and mowed vineyards, which reflects a gradient of soil disturbance, supports most of the variation in weed communities. Surprisingly, the type and level of fertilisation and herbicide use had little influence although herbicides have some effect on species traits in the summer surveys. Large-scale environmental variables, such as climatic conditions and landscape diversity, also have little influence. The small effect of landscape can be explained by the fact that our plots were globally located in vine-dominated landscapes with rather small variations. This contrasts with the strong influence of soil variables, especially along a resource gradient, from acidic sandy soils to clay soils with alkaline pH and higher organic matter content. We highlighted that specific trait values were associated with these disturbance and resource gradients, reflecting consistently the Grime's CSR strategies.

Our approach combined a global analysis at the vineyard scale (combining rows and inter-rows, and the two sampling dates) and separate analyses on the subsets of row versus inter-row flora on the one hand, and on the subsets of spring versus summer flora on the other hand. As expected, while the main associations between traits and agro-environmental variables were the same with all data sets, some effects were only detected in some subsets. The main gradient in both the rows and inter-rows was the opposition between spring and summer samplings as already highlighted in a previous study of vineyard weed communities (Fried et al., 2019). In the same vineyards, there is a turnover between small early flowering species in spring (*A. thaliana*, *C. glomeratum*, *Crepis sancta*, *Mibora minima* and *Muscari neglectum*) replaced by tall and late flowering species in summer (*Chenopodium album*, *Daucus carota* and *Erigeron canadensis*). The effect of some variables was only detected in the rows (e.g., herbicides or landscape diversity) or in the inter-rows (organic fertilisation and temperature). This was partly due to the specific location and timing of these agricultural practices: herbicides are sprayed in spring on the rows (see below *Disturbance gradients*) and organic fertilisation is mainly applied on the inter-rows. In diversified landscapes, woody species, surely spreading from neighbouring wood patches were found on the rows but not the inter-rows. This can be explained by the greater difficulty

of management on the row where tillage cannot be as efficient as it is on the inter-row and the use of herbicide at the registered rate does not eliminate woody species. The mechanical resistance of the perennial herbaceous inter-row to colonisation may also explain this pattern, while the row is always tilled or sprayed and species colonisation is therefore favoured by suppressing physical barriers and potential competitors. More surprisingly, some practices applied in the inter-rows (i.e., tillage) also showed a correlation with species traits of the rows. This might suggest that management on one area can influence the flora in the neighbouring area (either tillage in the inter-rows creates micro-disturbances in the rows, or species favoured by tillage on the inter-rows can spread to the rows) (Boinot et al., 2019).

### 4.1 | Disturbance gradients

The strongest structuring factors of the weed communities of the Bordeaux vineyards was the opposition between the tilled areas (inter-rows or rows) favouring annual species with a ruderal or a competitive-ruderal strategy and the mowed areas (inter-rows or rows) with hemicryptophytes with different types of competitive strategies (C, CS or CSR). Tilled areas were dominated by species such as *Lamium purpureum*, *S. vulgaris*, *P. annua*, *Stellaria media* and *V. persica* in spring, replaced by *Amaranthus retroflexus*, *Echinochloa crus-galli*, *Lactuca serriola* and *Setaria viridis* in summer. This result is consistent with other trait-based studies conducted in vineyards with either more annuals in tilled vineyards (Mainardis et al., 2020) or more R-strategist species on bare soils (including either tillage or herbicide treatments) (Hall et al., 2020). In line with this R-strategy, we also found a link between tillage and early flowering species (i.e., rapid life cycle) and high nutrient demand. To a lesser extent, the RLQ analysis suggested that SLA was also related to the soil tillage gradient. Weed communities with high SLA values were previously reported to be associated with vineyards with bare soils, either tilled or sprayed with herbicides (Hall et al., 2020). In fact, high SLA, which is positively correlated with relative growth rate, relates to a community with rapid completion of life cycle, well adapted to highly disturbed environment. At the vineyard scale, the number of herbicides treatment did not impact communities, probably because herbicide is applied on the row only and the row area represents a minor part of the field area. However, when looking at the row scale and in the summer samplings, we found that a higher number of herbicide treatments favoured small annuals with early flowering and a long flowering period. The fact that more relationships between herbicides and species traits were highlighted in summer is consistent with the fact that herbicides are applied in April after the first survey, so the species have been filtered out by this spring treatment only in the summer surveys. This illustrates the importance of positioning and utilising weed surveys appropriately according to the studied practices (Colbach et al., 2020). In our study, flowering period was measured at the species level, that is, it corresponds to species with successive cohorts with a rapid life cycle (*Capsella bursa-pastoris*, *Euphorbia helioscopia*, *P. annua* and *S. vulgaris*). The positive link between herbicides and flowering period

can be seen as a strategy to avoid herbicide pressure, a part of the population being able to complete its cycle between two treatments. On the opposite side of the gradient, mowing favoured hemicryptophytes with different kinds of competitive strategies (C, CS and CSR). Mowed areas are dominated by *Trifolium pratense*, *Lolium perenne*, *Dactylis glomerata*, *P. lanceolata* or *Poterium sanguisoba*. It has been shown that C- and CSR-strategists were associated with permanent vegetation cover in vineyards at the European scale (Hall et al., 2020), and other studies found that cover crops and/or mowing was associated with more conservative strategies with lower SLA (Kazakou et al., 2016), higher leaf area, deeper root depths index (Mainardis et al., 2020) and taller plant size (Kazakou et al., 2016; Mainardis et al., 2020). In our study, we did not take into account sown cover crops, as they were only temporary (winter), and were destroyed by tillage. Therefore, in spring, these inter-rows look much more like tilled inter-rows (with almost bare soil) than inter-rows with permanent vegetation managed by mowing.

## 4.2 | Resource gradient

Contrary to our initial expectations, the number of fertilisations or amendments was not associated with more nitrophilous species (Ellenberg-N) or species with rapid resource acquisition (high SLA values). Apart from a low positive correlation between organic amendments and annual species in the inter-rows and summer subsets, there was no effect of nutrient input. In our data set, it seems that the soil fertility gradient was more related to the soil characteristics opposing sandy acidic poor soils to clay alkaline richer soils. Interestingly, we found that seed mass, maximum plant height and Ellenberg-N to a lesser extent, were positively associated with the level of soil resource. The positive association of seed mass to soil fertility is a pattern that has been observed several times previously in natural habitats (May et al., 2013; Santini et al., 2017). DeMalach et al. (2019) demonstrated experimentally that the underlying mechanisms could be as follows: under low soil fertility (here sandy acidic soils), belowground competition is the dominant process shaping community structure. As belowground competition is size-symmetric, the growth rate advantage of small-seeded species results into higher fecundity and consequently, small-seeded species dominate the community. In contrast, under high soil fertility (here on alkaline clay soils), the dominant process determining relative growth rate becomes size-asymmetric competition for light. In such fertile soils, large-seeded species start with an initial size advantage, which further increases with time since they capture most of the light. Under these conditions, large-seeded species suppress the growth of the small-seeded species, grow faster, produce more seeds per individual and dominate the community. This mechanism is consistent with the results of our study where large-seeded species on fertile soils were also tall species with high Ellenberg-N values conferring a high competitive ability (e.g., *Elytrigia repens*, *Malva sylvestris* and *Rumex* spp.).

To summarise, the effect of tillage is very consistent across studies, and we confirmed here that tillage favoured species with a ruderal

strategy, an annual life cycle (Guerra et al., 2021; Hall et al., 2020; Mainardis et al., 2020) and an early flowering onset (Bopp et al., 2022; Guerra et al., 2021). The picture is more mixed for herbicides and mowing suggesting that they may also depend on other factors. For example, in summer samplings, we found that herbicides selected small-sized early flowering species as found by Bopp et al. (2022) in three other wine regions of France, while other studies found that species in sprayed plots were rather high-sized (Guerra et al., 2021; MacLaren et al., 2019) and late flowering (Guerra et al., 2021). This could also be explained by the existence of several viable strategies in sprayed vineyards, a pure ruderal strategy or a combined competitive-ruderal strategy, which implies partly different trait values. Finally, both Guerra et al. (2021) and Hall et al. (2020) highlighted that mowing selects hemicryptophytes, the former with a stress-tolerant strategy, the latter with a competitive strategy. Our results partly reconcile these two studies since both hemicryptophytes with a C and CS strategy were selected by mowing, showing that again several strategies are viable. Actually, mowing has been shown to select for both traits related to competitive strategy as high stature (Bopp et al., 2022; Kazakou et al., 2016; Mainardis et al., 2020), but also trait values compatible with both C and S strategies such as high seed mass (Bopp et al., 2022; MacLaren et al., 2019) and low SLA values (Bopp et al., 2022; Guerra et al., 2021; Hall et al., 2020; Kazakou et al., 2016; Mainardis et al., 2020). In our study, there was a further separation between C- and S-strategists along a soil resource gradient that had a stronger structuring effect than fertilisation practices. However, the trait values selected on the fertile side of this gradient (high size and high seed mass) were consistent with the effects of irrigation found by Guerra et al. (2021).

## 5 | CONCLUSIONS

This study is one of the first to confirm that weed vegetation can be summarised by specific trait values and consistent strategies along two orthogonal gradients of disturbance and resource availability in relation to management practices and soil characteristics. Life forms, flowering phenology and SLA were mostly associated with the level of disturbance while plant height and seed mass were more related to competition-related mechanisms associated with soil fertility. Based on knowledge of the soil characteristics, it becomes possible to predict which type of weeds (major traits and CSR strategy) will occur according to the combination of practices applied on the rows and inter-rows.

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### CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author.

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#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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## **Sous-partie 2 - Réponse des communautés adventices des vignobles aux pratiques de gestion du sol et au pédoclimat, dans le temps**



Travail du sol en traction animale

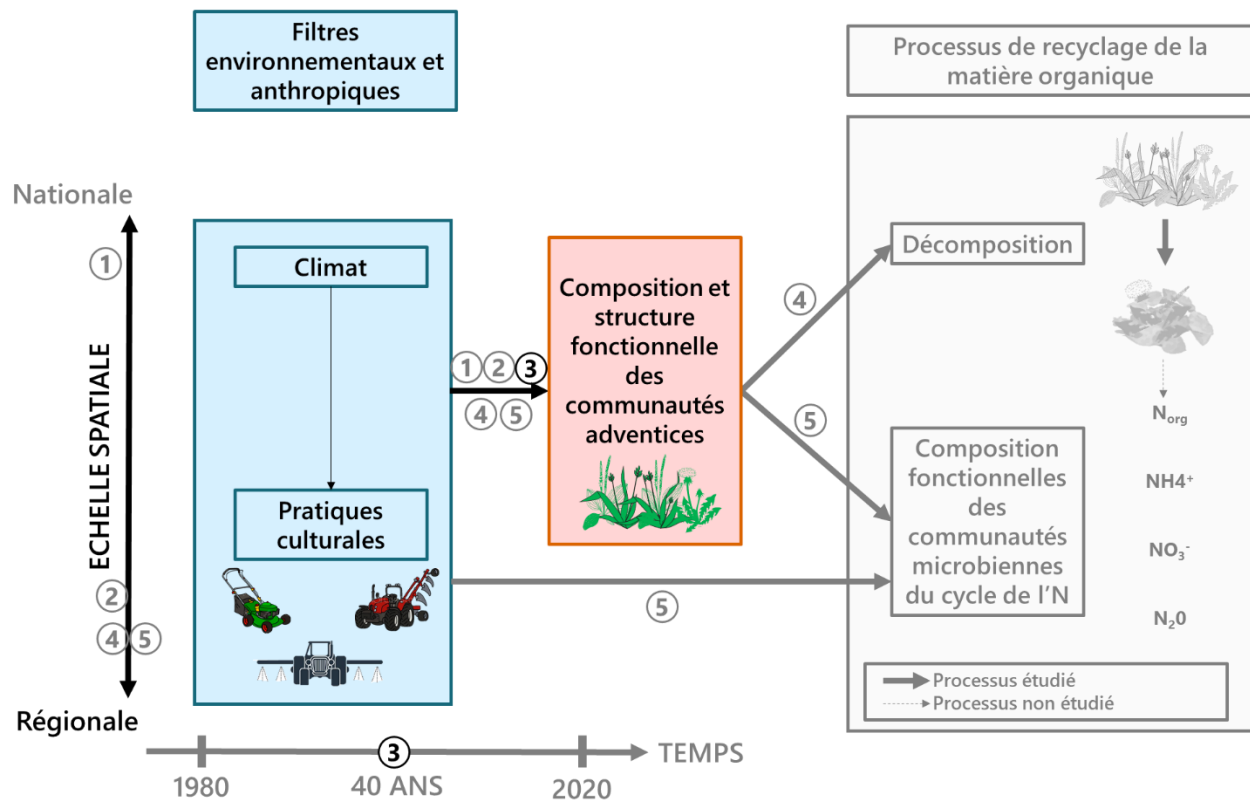
Photo de Régis Aymé (quelque part dans l'Aude, 1964)



# Chapitre 3 - 40-year changes in weed community properties induced by management and climate change in Mediterranean vineyards

Bopp M.-C., Kazakou E., Metay A., Maillet J., Quidoz M.-C., Genty L., Fried G.

Article en cours de préparation







## **Présentation du chapitre**

Ce chapitre est basé sur un jeu de données de relevés floristiques (n=374) de la région du Montpelliérais (40 parcelles de vignes), observés en 1978, 1979, 2020 et 2021. **L'objectif de cette étude est de comparer les propriétés fonctionnelles des communautés adventices des années 1980s et des années 2020s et d'expliquer les différences observées par l'évolution historique des pratiques de gestion des adventices et le changement climatique.**

**Les hypothèses de cette étude sont:**

- (i) Le changement climatique est significatif des années 1980s à 2020-2021 et il favorise des communautés adventices stress-tolérantes,
- (ii) Les pratiques de gestion des adventices sont devenues plus intégrées des années 1980s à 2020-2021 et ont sélectionné des communautés adventices moins rudérales.

En quatre décennies, l'amplitude annuelle des températures (c'est-à-dire la différence entre les températures moyennes du mois le plus chaud et du mois le plus froid) a augmenté de 1,2°C et les températures estivales de 2°C (Figure 20). La gestion des adventices s'est diversifiée au fil du temps avec l'adoption de la tonte qui a remplacé le désherbage chimique des inter-rangs. Les communautés adventices des années 2020s sont 41 % plus abondantes et 24 % plus diversifiées que les communautés des années 1980s (Figure 20). Les communautés actuelles sont composées de plus d'annuelles (57 % des espèces annuelles dans les années 1980s contre 80 % dans les années 2020s), avec une capacité de propagation latérale et une masse de graines plus faibles, et sont composées de moins d'espèces C<sub>4</sub>. Elles présentent un SLA plus élevé, une teneur en matière sèche foliaire (LDMC) plus importante, une surface foliaire plus faible et fleurissent plus tôt et plus longtemps que les communautés adventices des années 1980s. Le changement climatique a induit des communautés plus tolérantes au stress dans les années 2020s, tandis que la diversification des pratiques de gestion des adventices a filtré des communautés moins compétitives (Figure 20).

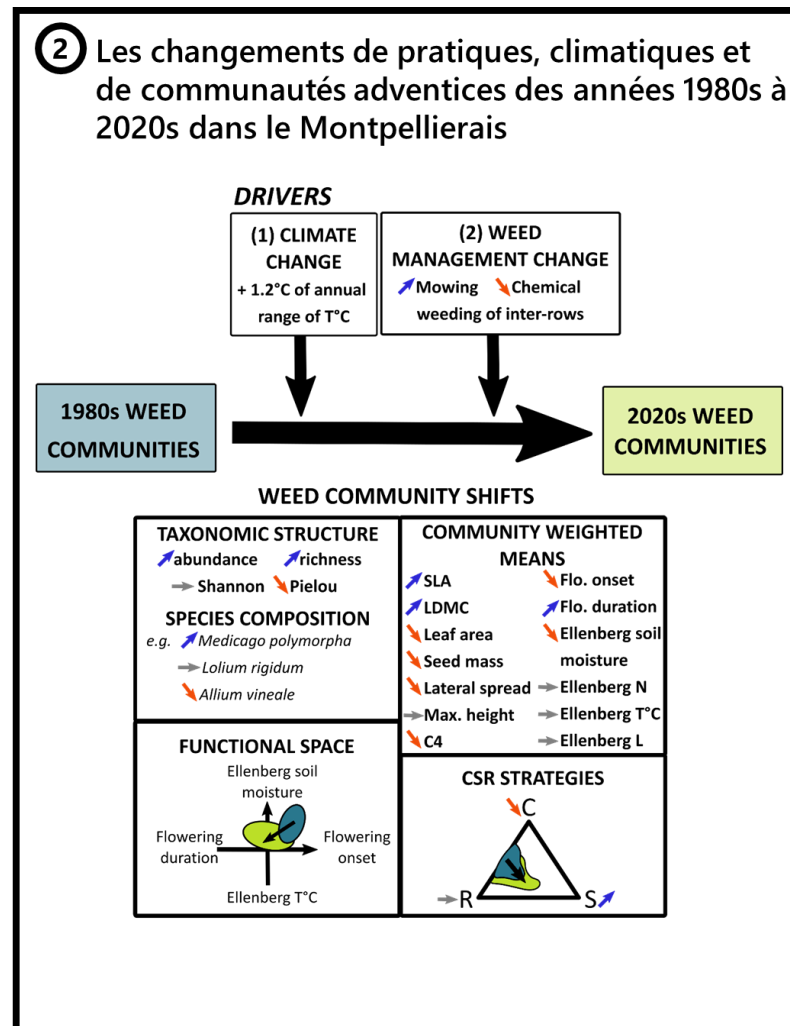
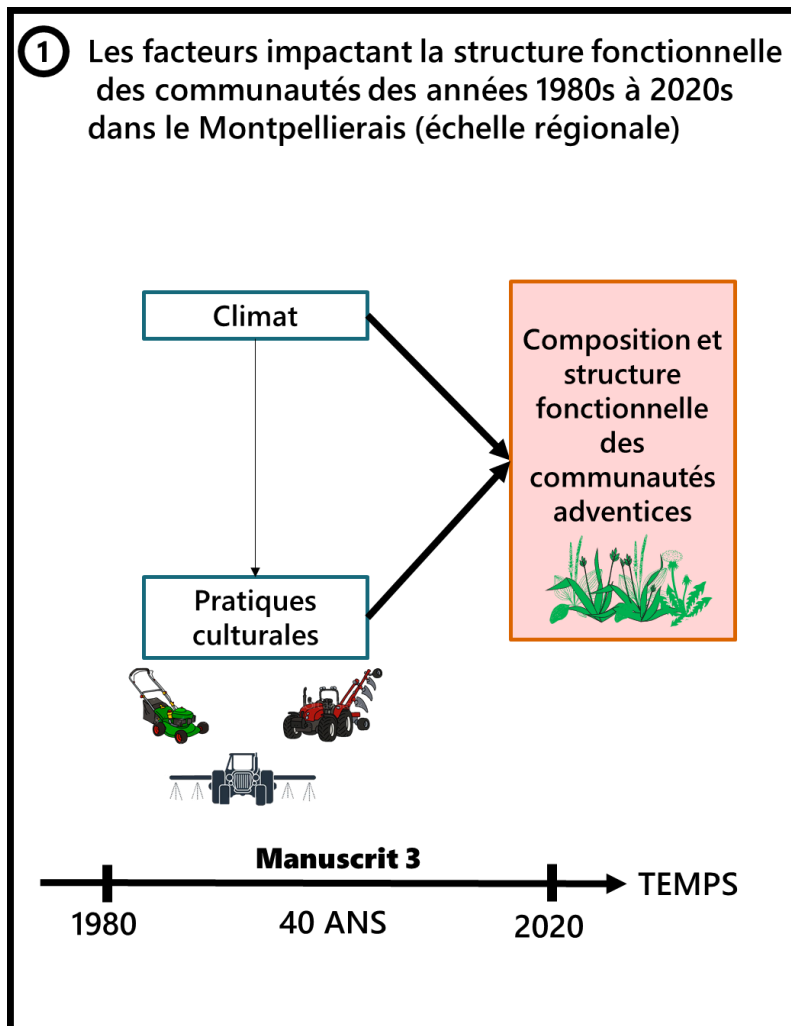


Figure 20 Résumé graphique du chapitre 3. (1) Le changement climatique et les changements de pratiques culturales ont significativement impacté les propriétés fonctionnelles des communautés adventices des années 1980s à 2020s. (2) Le changement climatique a été significatif avec une augmentation de 1.2°C de l'amplitude thermique annuelle. Les pratiques de gestion des adventices ont évolué vers plus de tonte et moins de désherbage chimique sur l'inter-rang. (3) Les communautés actuelles sont plus abondantes, plus riches et moins équitables. Elles ont des SLA, LDMC et durée de floraison plus élevés et des aires foliaires, des masses de graines et des capacités de propagation latérale plus faibles. Elles sont composées de plus de C4 que dans les années 1980. Elles ont de moindre besoin en eau. L'adoption de la tonte et les pratiques plus intégrées actuelles ont favorisé des communautés moins compétitives tandis que le changement climatique a favorisé des communautés plus stress-tolérantes.

## **TITLE**

# **40-year changes in weed community properties induced by management and climate change in Mediterranean vineyards**

## **ABSTRACT**

Spontaneous plant communities have undergone considerable constraints due to human-mediated changes. Weed communities located in Mediterranean vineyards have experienced significant changes in agro-environmental conditions as weed management strongly evolved these past decades and as climate change in the Mediterranean exceed global trends for most climate variables. In this study, we quantified to which extent weed communities have shifted from the 1980s to the 2020s in response to climate and weed management changes, using a historic network of 40 Mediterranean vineyards and 374 floristic surveys in Montpellier, France. In four decades, the annual range of temperatures (*i.e.* the difference between the warmest month's and the coldest month's mean temperatures) increased by 1.2°C and the summer temperatures by 2°C. Weed management diversified over time with the adoption of mowing that replaced the chemical weeding of inter-rows. Current weed communities were 41% more abundant, 24% more diverse and with a less even distribution of abundance across species than the 1980s communities at the vineyard level. Current communities were composed of more annuals (57% of annual species in the 1980s versus 80% in the 2020s) with lower lateral spread ability and seed mass and were composed of fewer C<sub>4</sub> species. They had higher community-weighted specific leaf area, higher leaf dry matter content, lower leaf area and flowered earlier and longer than 1980s weed communities. Climate change induced more stress-tolerant communities in the 2020s while the diversification of weed management practices over time filtered less competitive communities. This study shows that weed communities are adapting to climate change and that weed management is a strong lever for action to model more diverse and functional weed communities in the future.

## **KEYWORDS**

Climate change, CSR strategies, Mediterranean vineyards, trait-based approach, weed community, weed management change, 40-years temporal changes.

# INTRODUCTION

Spontaneous plant communities have undergone considerable constraints due to human-mediated changes at global (*e.g.* climate change) and regional scales (*e.g.* land use change) (Inderjit et al., 2017). At the global scale, climate change results in higher temperatures, altered precipitation, higher frequency of extreme weather events and increased level of CO<sub>2</sub> (Peters et al., 2014). The Mediterranean area has been identified as one of the most sensitive regions to climate change, with a predicted severe decline of precipitations, while higher precipitations are expected in other parts of the world (Tuel and Eltahir, 2020). Consequently, climate change is expected to impact disproportionately Mediterranean vegetation compared to other regions of the world (Newbold et al., 2020). The projections of the effect of climate change on plant communities are severe: decreased species richness, reduction of the species range, shifts toward a higher proportion of annual species in communities and a lower proportion of forbs (Pfeifer-Meister et al., 2016; Sala et al., 2000). These changes in plant composition can ultimately alter many ecosystem processes (Cardinale et al., 2012). This changing global filter also interacts with regional filters like human management (Bourgeois et al., 2021) that has become more pronounced during the last decades. In the last 50 years, agriculture intensification has exerted strong selection pressures on spontaneous plant communities co-occurring with crops (*i.e.* weeds), favouring communities adapted to a high level of disturbance and resources (Bourgeois et al., 2019). Consequently, weed diversity has dramatically decreased in arable lands these past decades due to changes in weed management including herbicides and fertilisation input (Cirujeda et al., 2011; Fried et al., 2009a, 2016; Richner et al., 2015; Storkey et al., 2012, 2021).

In agrosystems, the temporal changes in plant community were mostly described in annual cropping systems while few studies have investigated flora shifts in less disturbed systems like perennial cropping systems. Mediterranean vineyard weed communities are particularly relevant models to study flora shifts. Indeed, agricultural practices of vineyards strongly evolved from the late 1970s to nowadays. At the end of the 1970s, herbicides appeared and started to be applied widely on both the rows and the inter-rows of vines (*i.e.* the free space between the rows of vines) (Maillet, 1981). This constituted an abrupt change in environmental conditions resulting in drastic changes in the flora (Maillet, 1992). For instance, annual species decreased in abundance and frequency while

some perennial species coming from the garrigue (*i.e.* low Mediterranean scrubland) and favoured by triazine-based herbicides (*e.g.* *Rubia peregrina*), colonised the vineyards (Maillet, 1992). In the 2000s, the awareness of the detrimental effects of herbicides on the environment (*e.g.* water quality) has led farmers to limit their use. Superficial tillage and mowing gradually replaced herbicide use in the inter-rows, leading to more integrated weed management (Fernández-Mena et al., 2021). Moreover, in 2021, the use of glyphosate was forbidden in the inter-rows of vineyards in France (ANSES, 2020). However, chemical weeding of the rows is still widespread in French Mediterranean vineyards (Bopp et al., 2022a).

Trait-based approaches provide a relevant framework to better understand how weed communities shift in response to climate and management changes (Richner et al., 2015). Functional trait values at the community level, as known as ‘functional markers’ (Garnier et al., 2004), respond to environmental filtering (*e.g.* climate change) (Lavorel and Garnier, 2002) and anthropogenic drivers (*e.g.* agricultural practices) (Booth and Swanton, 2002; Damour et al., 2018; Navas, 2012). This approach assumes that only certain species with specific trait values will persist within communities in particular climate and management conditions. Mediterranean studies of trait patterns along aridity gradients revealed that climate change would filter communities with a more resource-conservative strategy: communities with smaller species, shorter flowering duration, lower leaf area and specific leaf area (SLA) than current communities (Costa-Saura et al., 2016; de la Riva et al., 2018; Nunes et al., 2017). Moreover, high temperatures and frequent drought would favour C<sub>4</sub> weed species (Korres et al., 2016), late-emerging and thermophilic species (Peters et al., 2014). However, rising CO<sub>2</sub> atmospheric pressure is expected to favour C<sub>3</sub> species. Thus, the impact of climate change on photosynthetic pathway is not entirely clear (Peters et al., 2014).

Weed management practices can be considered as anthropogenic disturbances and can be classified according to their intensity and frequency (Gaba et al., 2014; Kazakou et al., 2016). For instance, chemical weeding and tillage represent both high-intensity disturbances as they destroyed the whole biomass (Kazakou et al., 2016). In contrast, mowing would be a lower intensity disturbance as this practice removes the biomass partially (MacLaren et al., 2019). Recent synchronic studies (*i.e.* comparing simultaneously vineyards with different managements) demonstrated the

strong filtering effects of management on weed communities in vineyards (Kazakou et al., 2016; MacLaren et al., 2019). More precisely, mowing favoured more conservative weed communities with more perennial, higher seed mass, higher stature, lower specific leaf area (SLA) and higher leaf dry matter content (LDMC) than communities managed with other practices like tillage (Bopp et al., 2022b; Fried et al., 2022; Guerra et al., 2021; Hall et al., 2020; Kazakou et al., 2016; Mainardis et al., 2020). In contrast, tillage and chemical weeding favoured more acquisitive communities composed of more annuals and late-flowering species with higher SLA and lower LDMC (Bopp et al., 2022b; Fried et al., 2022; Hall et al., 2020). The CSR scheme of Grime (1977) is an integrative approach to studying adaptative strategies that species use to cope with two constraints: (i) stress related to the shortage of resources (*e.g.* water stress related to climate change in the Mediterranean area) and (ii) disturbance related to the sudden destruction of biomass (*e.g.* weed management practice as tillage, mowing, chemical weeding). The CSR scheme describes 3 main species strategies: (i) stress tolerators (S) in resource-poor habitats with low disturbance, (ii) ruderals (R) in resource-rich and highly disturbed environments (*e.g.* agrosystems) and (iii) competitors (C) in highly productive habitats with low-stress intensity and disturbance. If weeds are mostly ruderals in relation to the fact that cultivated habitats are by definition regularly disturbed by tillage (Bourgeois et al., 2019; Mahaut et al., 2020), a recent study demonstrated that the proportion of CSR strategies in weed communities changed according to the weed management practice used (Fried et al., 2022). For instance, mowing favoured communities with more competitive strategies while tillage favoured species with more ruderal strategies. Climate change might also modify the relative proportion of species CSR strategies within the communities over time (MacLaren et al., 2020). For instance, under climate change, weeds with stress tolerator strategies are more likely to occur (Korres et al., 2016). If recent synchronic studies exist in weed functional response to management (*e.g.* MacLaren et al. 2019, Hall et al. 2020), no study, to our knowledge, has yet been conducted on weed community functional changes over time in vineyards.

In this study, we quantified to which extent weed communities have shifted from the 1980s to the 2020s in response to changes in climatic conditions and weed management practices, using a historic network of 40 Mediterranean vineyards in Montpellier, France (Figure 1). First, we assessed climate change intensity and characterise changes in weed management practices in the network



(Figure 1). Then, we described shifts of taxonomic and functional weed community structure after four decades using 374 floristic surveys that were performed during two years at each period (1978, 1979, 2020, 2021) and at 3 seasons (March, June, October). Finally, we tested if climatic conditions and weed management practices drove changes in weed community structure between the 1980s and the 2020s (Figure 1). We hypothesised that climate change has already resulted in significant changes in temperatures and precipitation between 1980s and 2020s. We expected that weed management evolved from chemical weeding to tillage and mowing. We hypothesised that climate change would favour species with more water-conservative traits (*e.g.* C<sub>4</sub> metabolism, small leaf area, high LDMC) and stress-tolerant strategies. Moreover, we expected that the decrease in herbicide use replaced by tillage and mowing would favour more conservative and competitive strategies for two reasons: (i) mowing is a lower intensity disturbance than chemical weeding, filtering more conservative strategies than other management practices and (ii) consequently, weed biomass and competition for resource might be higher in mowed communities, selecting competitive species.

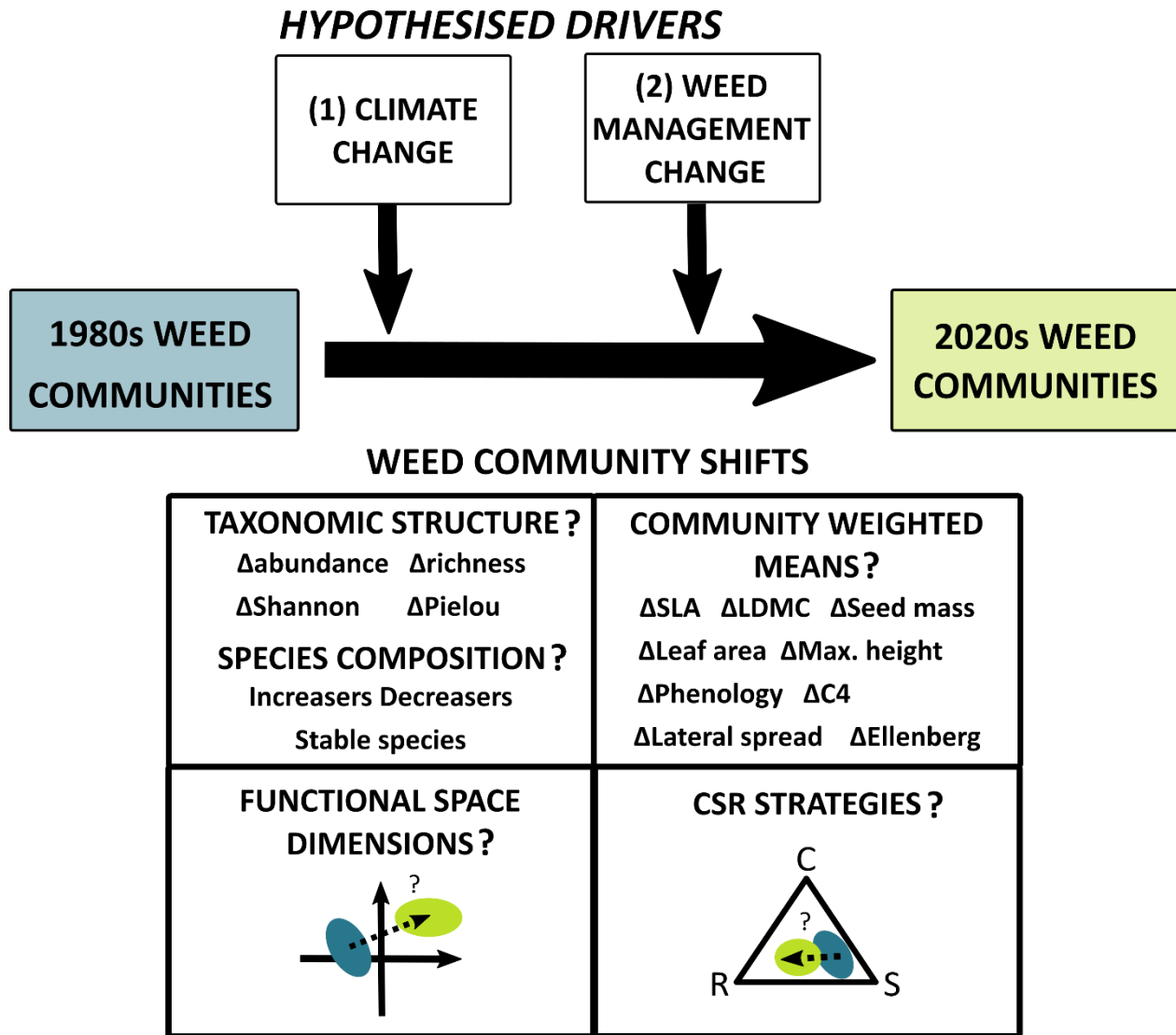


Figure 1 Hypothesised drivers of weed community shifts from 1980s to 2020s. Weed community shifts from the 1980s to the 2020s will be characterised by the changes in (i) taxonomic structure (abundance, richness, Shannon and Pielou index), (ii) species composition (increasers, decreasees, stable species), (iii) 13 community weighted means (CWM), (iv) coordinates on the first four axes of a Principal Component Analysis based on CWM, (v) the CSR scores of the weed communities. We hypothesised that two main drivers would impact weed community shifts: (i) climate change and (ii) weed management changes during the four decades between the two floristic survey periods.

# MATERIALS AND METHODS

## 1. Climate, soil and weed management characterisation of the historical vineyard network

The network was composed of 40 vineyards located around Montpellier, France (Figure 2). This network was first set up in 1978 to study management effects on weed community composition (Maillet, 1981). The vineyards are located in a Mediterranean climate characterised by warm temperatures (14°C mean annual temperatures on average from 1978 to 2021), irregular rainfall (814 mm per year) and dry summers (88% of annual precipitation occurs during the other seasons). Soil textures of vineyards varied along a North-East/South-West gradient determined by the distance to the Mediterranean Sea: from sandy vineyards nearby the Sea to loamy and clay/loamy soils in further northeast vineyards (Data S1).

To characterise climate change, variables describing seasonal and annual climate were extracted from the estimations obtained by SAFRAN interpolation method (Système d'analyse fournissant des renseignements atmosphériques à la neige) on an 8 km × 8 km grid (Durand et al., 1993) from 1971 to 2021. Eleven variables were selected: mean seasonal temperatures and rainfall (spring, summer, autumn and winter), growing season length (GSL) (*i.e.* the number of days in a year with daily mean temperature is above 5°C during at least 6 consecutive days), numbers of frost days and annual range of temperatures (*i.e.* the difference between the warmest month's and the coldest month's mean temperatures), and were averaged over 5 different decades from 1971 to 2021 (1971-1980 ; 1981-1990 ; 1991-2000 ; 2001-2010 ; 2011-2021) (Table 1). Due to the SAFRAN grid, 31 neighbouring vineyards on 40 shared the same climate data at least with another vineyard: 20 squares of 8x8 km<sup>2</sup> with different climate data were used for the 40 vineyards of the network.

To characterise changes in weed management practices of the rows and the inter-rows from 1978 to 2021, we conducted two interviews with each farmer of the network. The first interview was realised in June 2020 on the weed management practices applied from 1978 to June 2021 (45 minutes) and the second one was conducted in June 2021 to collect information about the more recent weed management practices (15 minutes). The questionnaire was composed of 61 questions

with open and multiple-choice answers divided into three sections: (i) farm characteristics (area, wine valorisation, labels), (ii) vineyard characteristics (topography, vine density, grape variety, fertilisation, manure, irrigation) and (iii) weed management practices of rows and inter-rows from 1978 to 2021 (chemical weeding, tillage and mowing). Based on their answers and our hypothesis regarding the relationships between the functional structure of spontaneous vegetation and management, we considered the five following binary practice variables: (i) chemical weeding of rows, (ii) chemical weeding of inter-rows, (iii) tillage of rows, (iv) tillage of inter-rows and (v) mowing of inter-row. Each variable had two possible values: 0, not applied ; 1, applied. Indeed, we downgraded the information of the practice variables (for instance, we did not considered the number of management interventions) to be able to describe weed management trajectory over time. To define the trajectory of the weed management practices of each vineyard, we used the values of these five variables over five different periods: 1978-1979 (the initial weed management practices) ; 1980-1990 ; 1991-2000 ; 2001-2010 and 2011-2021 (the final weed management practices).

## **2. Weed community composition in the 1980s and the 2020s**

Weed community composition was determined in 1978 and 1979 (as ‘1980s communities’ hereafter) (Maillet, 1981) and in 2020 and 2021 (as ‘2020s communities’) at 3 different seasons (late winter, early summer and autumn). However, because of the summer drought in 1978, the autumn floristic surveys were not done that year (Maillet, 1981). Therefore, to have equivalent data sets for the 1980s and 2020s periods, we did not use the floristic surveys of Autumn 2020. Moreover, in March 1978 and March 2020, only 27 plots were surveyed. In total, the data set was composed of 374 floristic surveys (2 periods x 27 vineyards x 1 season + 2 periods x 40 vineyards x 4 complete seasons). To compare the floristic compositions over the two periods, we applied the same method of floristic surveys. To control the ‘observer effect’, we conducted several floristic surveys in 2020 with Jacques Maillet, who conducted the floristic surveys in the 1980s. No major biases were observed during these floristic surveys. In each vineyard, a rectangular area of 400 m<sup>2</sup> (40m x 10m) was delimited (4 inter-rows and 3 rows of the same length).

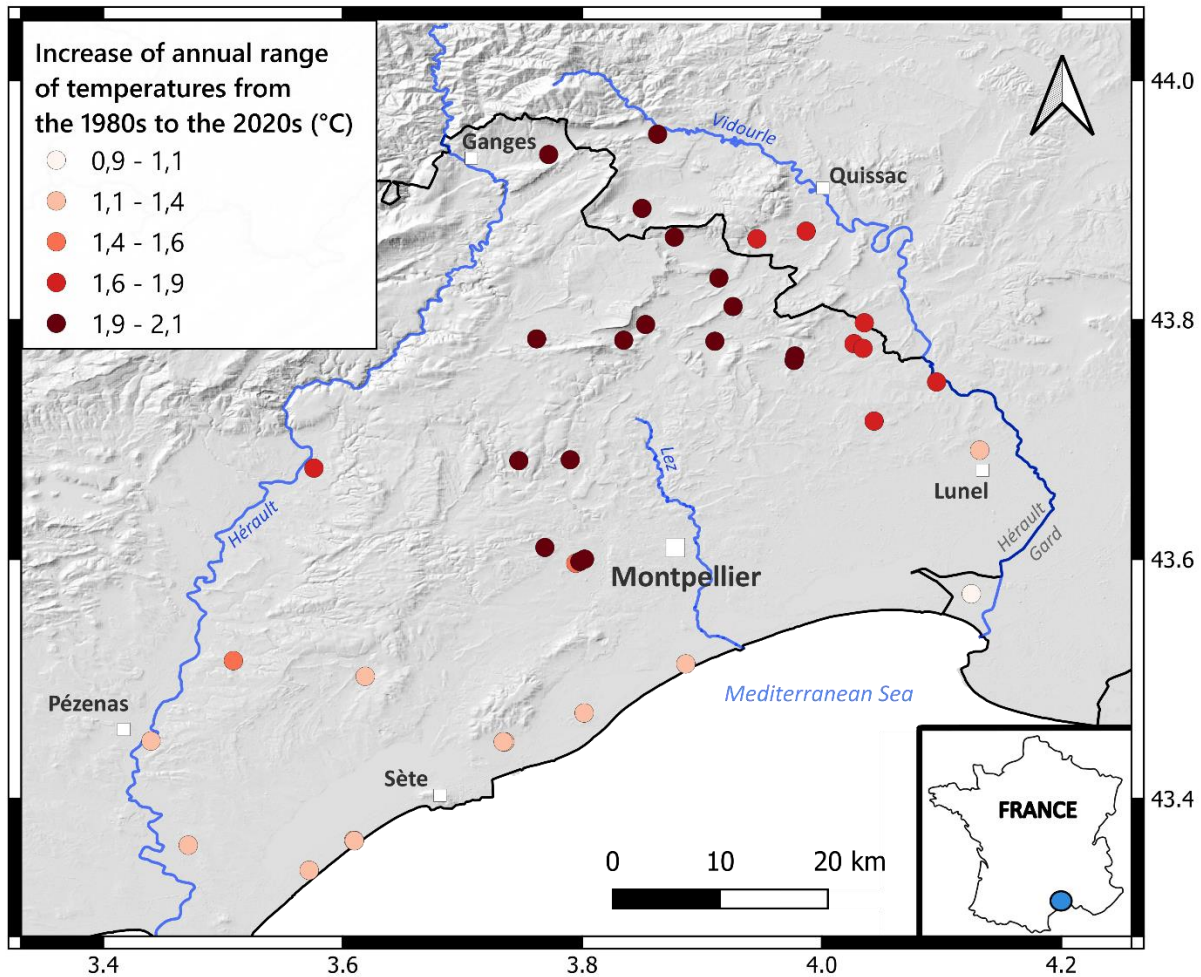


Figure 2 Geographical distribution of the increase of annual range of temperatures from the 1980s to the 2020s experienced by the 40 vineyards of the network, Montpellier, France. Each dot is a vineyard and its colour represents the extent of the increase in the annual range of temperatures: from light red for low increases to dark red for high increases. The dark lines represent the departments outlines. The blue lines represent the main rivers of the region. The values displayed on the frame surrounding the map are the latitudinal and longitudinal coordinates.

To estimate species abundance, we used five abundance classes developed in Barralis (1976): ‘1’, less than 1 individual/m<sup>2</sup>; ‘2’, 1–2 individuals/m<sup>2</sup>; ‘3’, 3–20 individuals/m<sup>2</sup>; ‘4’, 21–50 individuals/m<sup>2</sup>; ‘5’, more than 50 individuals/m<sup>2</sup>. We transformed these scores into a quantitative scaling using the median of the range of each density class as followed: ‘1’, 0.5 individual/m<sup>2</sup>; ‘2’, 1.5 individuals/m<sup>2</sup>; ‘3’, 11.5 individuals/m<sup>2</sup>; ‘4’, 35.5 individuals/m<sup>2</sup>; ‘5’, 75 individuals/m<sup>2</sup>. A list of species and distinct abundance scores were noted at the plot level. For each community, we computed the richness, the abundance (*i.e.* the sum of the abundance scores of each species), the Shannon diversity index and

the Pielou's evenness index which is the ratio between the Shannon index and the logarithm of the community richness (Pielou, 1966).

### **3. Functional properties of the 1980s and 2020s weed communities**

Thirteen plant traits were selected to capture plant responses to climate change and weed management changes. Three traits of the Leaf-Height-Seed (LHS) strategy scheme were selected (Westoby, 1998): (a) specific leaf area (SLA,  $\text{m}^2 \cdot \text{kg}^{-1}$ ) which is the light-catching area deployed per unit of previously photosynthesized dry mass related to the speed of resources acquisition (Wright et al., 2004), (b) maximum height (m) which expresses the possible amount of growth in an undisturbed environment related to light and nutrient acquisition (Westoby et al., 2002), (c) seed mass (g) which represents the “colonisation-competition” trade-off (Moles and Westoby, 2006). Leaf area was also selected as a good *proxy* for the competitive abilities of plants. The lateral spread was also selected as a response trait to disturbance. This qualitative trait represents species' abilities to develop horizontally (species with rhizomes or forming tussocks); it is rated as followed: “1”, therophytes ; “2”, perennials with compact unbranched rhizomes or forming small tussocks (less than 100 mm in diameter) ; “3”, perennials with a rhizomatous system or tussocks reaching from 100 to 250 mm ; “4”, perennials reaching a diameter of 251 to 1000 mm. Leaf Dry Matter Content (*i.e.* the ratio between leaf dry mass and leaf fresh mass) was selected as a *proxy* of plant investment in leaf structure. Photosynthesis pathways (C<sub>3</sub>/C<sub>4</sub>) were assessed to identify the species with water-saving photosynthesis (C<sub>4</sub> plants) (Pyankov et al., 2010). Phenology was characterised through the months of flowering onset and the number of months of flowering. Species resource requirements were characterised through four Ellenberg indices: light (EIV\_L), temperature (EIV\_T), soil moisture (EIV\_F) and nitrogen (EIV\_N). Raunkiær plant life forms were included.

Leaf area, SLA and LDMC were measured on the weed species present in the 2020s communities. The other traits were extracted from different databases: Seed Information Database for seed mass (Royal Botanic Gardens Kew, 2021), *Flora Gallica* for maximum height (Tison and De Foucault, 2014), lateral spread from Hodgson et al (1995) supplemented by expert opinion (G. Fried, pers.

com.), Baseflor for flowering onset, duration of flowering and the four Ellenberg indices (Julve, 1998). Flowering onset and duration of flowering are quantified at the population level and not at the individual level (*i.e.*, a long flowering duration does not mean that individuals of that species can flower during a long period but that different individuals of that species cover together a long period of flowering). Photosynthetic pathways were extracted from Pyankov et al. (2010).

To scale up the trait values from the species level to the community level, we calculated Community Weighted Means (CWM, *i.e.* average of the trait values of species present in a community, weighted by their relative abundances) (Garnier et al., 2004) using at least 80% of the most abundant species of the weed communities in the calculation. Considering the nature of the lateral spread variable (*i.e.* quantitative and discrete), we chose to compute the median of the lateral spread values within the communities. Moreover, for the photosynthetic pathway trait (C<sub>3</sub>/C<sub>4</sub>), we computed the percentage of C<sub>4</sub> species' abundance within the communities.

Based on the CWM of SLA, LDMC and leaf area, we calculated the competitiveness (C), stress-tolerance (S) and ruderal (R) scores following Pierce et al (2017) who developed CSR ordination of species based on multivariate analysis, which was validated at the community level (Li and Shipley, 2017).

## **4. Data analyses**

### *4.1. Description of climate, weed management and weed community functional structure using multivariate analyses*

To describe climate and weed management changes over the four decades, we computed (i) a Principal Components Analysis (PCA) based on climate characteristics per decade from the 1980s to the 2020s and (ii) a Principal Coordinates Analysis (PCoA) based on weed management characterisation per decade from the 1980s and 2020s that characterised the trajectory of weed management. In addition to defining the weed management trajectory during four decades, 2020s weed management was also characterised. A PCA was performed on the following agricultural

practice variables averaged over the 2015-2021 period (Figure S1): (i) the annual number of chemical weeding, tillage and mowing applied at the row of vines and the inter-row (*i.e.* the free space between the rows of vines) level, (ii) fertilisation input and soil amendment. To group the vineyards according to their 2020s practices, hierarchical clustering was then performed on the principle components. Vineyards were classified into four clusters (Figure S1). Cluster ‘Chem’ gathers four vineyards with chemical weeding of both rows and inter-rows. Cluster ‘Till.IR.Chem.R’ regroups 19 vineyards with tilled inter-rows and chemically weeded rows. Cluster ‘Mow.IR.Till.R’ gathers 11 vineyards with mowed inter-rows and tilled rows. Cluster ‘Till’ groups six vineyards with tilled rows and inter-rows. To characterise the functional space of the weed communities, a PCA was also performed on the CWM of the 13 traits of the 1980s and 2020s communities. To select a parsimonious number of dimensions which represents well the functional space, we used the elbow inflexion point method on the Area Under the Curve (AUC) and the Mean Absolute Deviation (MAD) following Mouillot et al. (2021).

#### *4.2. Comparison of weed structure and composition of the 1980s and the 2020s*

Two different datasets were used for data analyses (Figure 3). The first one is the ‘full dataset’ composed of the 374 floristic surveys from the 1980s and the 2020s. This dataset was used to test the significance of the difference in means of taxonomic indices (abundance, richness, Shannon, Pielou), Raunkiær plant life-forms, CWM and CSR scores over time. Using the full dataset ( $n=374$ ), we fitted linear mixed models with the period (1980s, 2020s) as a fixed effect and the season (March, June, October), the year (1978, 1979, 2020, 2021) and plot identity as random effects. An ANOVA was performed on these models to test fixed effect significance. Post-hoc Tukey and Wilcoxon tests were then computed to assess the direction of the changes in functional properties of weed communities from the 1980s to 2020s. Moreover, the species that increased, decreased or remained stable in abundance and frequency at the network level from the 1980s and the 2020s were identified using indices of relative changes following this formula:  $(\text{Indice}_{2020s} - \text{Indice}_{1980s}) / (\text{Indice}_{2020s} + \text{Indice}_{1980s})$ .



#### 4.3. Identification of the drivers of weed community structure shifts over time

The second dataset was built to test if climate and management changes explained the changes in taxonomic and functional properties of weed communities (Figure 3). To build an ‘explaining’ dataset, we averaged the functional and taxonomic metrics over the two years for each period: from five floristic surveys per period (*e.g.* for 1980s, March 78, 79, June 78, 79 and October 79) to three floristic surveys per period (*e.g.* March 1980s, June 1980s, October 1980s). Then, each season of each period was comparable with the season of the other period (*e.g.* March 1980s with March 2020s). Then, this ‘explaining’ dataset was composed of 120 taxonomic and functional shifts of communities from the 1980s to the 2020s: 40 vineyard community shifts x 3 seasons (Table 1). Due to missing data on weed management practices (*e.g.* farmers that had passed away or were not reachable), the dataset without missing data was finally composed of 108 functional shifts. We used two different ways of computing indexes of changes: (i) for comparing coordinates of the CWM in the functional PCA, we computed the difference between the coordinates in the 2020s and the coordinates in the 1980s for each selected axes of the multivariate analysis (Table 1) and (ii) for comparing ‘raw values’ of different metrics (CWM, CSR scores, annual temperature range, abundance, richness, Shannon and Pielou indices), we computed indices of relative changes using the following formula:  $(\text{Indice}_{2020s} - \text{Indice}_{1980s}) / (\text{Indice}_{2020s} + \text{Indice}_{1980s})$  (Table 1).

We selected the climate and management drivers that explained most of the climate and management changes over the four decades from the PCA based on climate characteristics and from the PCoA based on management and tested if these drivers explained the shifts of weed communities over time. As a *proxy* of climate change, we selected the changes in the annual range of temperatures between the 1980s and the 2020s (*i.e.* the difference between the warmest month's and the coldest month's mean temperatures). To describe weed management trajectory, we used three variables: (i) the number of decades since herbicide use was stopped, (ii) the number of decades since mowing was used and (iii) the additional number of different management practices applied at the plot level from the 1980s to the 2020s, as a *proxy* of the trajectory toward more integrated weed management (*e.g.* if tillage was the only management practice used in the 1980s and if mowing and tillage were used in 2020s, the value would be ‘1’ additional weed management practice applied). To describe

current weed management, we selected the categorical variable describing 2020s weed management practices with four different groups (**‘Chem’**: vineyards with chemical weeding of both rows and inter-rows ; **‘Till.IR.Chem.R’**: vineyards with tilled inter-rows and chemically weeded rows; **‘Mow.IR.Till.R’**: vineyards with mowed inter-rows and tilled rows ; **‘Till’**: : vineyards with tilled rows and inter-rows) (Table 1). Using the ‘explaining’ dataset (n=108), we fitted fitting linear mixed models to explain the shifts in CWM, taxonomic indices (abundance, richness, Pielou, Shannon) and CSR scores over time by the selected drivers of climate and management changes as fixed effects and with the season and plot identity as random effects. The selection of models was done based on the corrected Akaike Information Criterion (AICc) with the *dredge* function from the *MuMIn* R package (Burnham and Anderson, 2002). All data analyses were carried out using R version 4.1.1 (R Core Team, 2021).

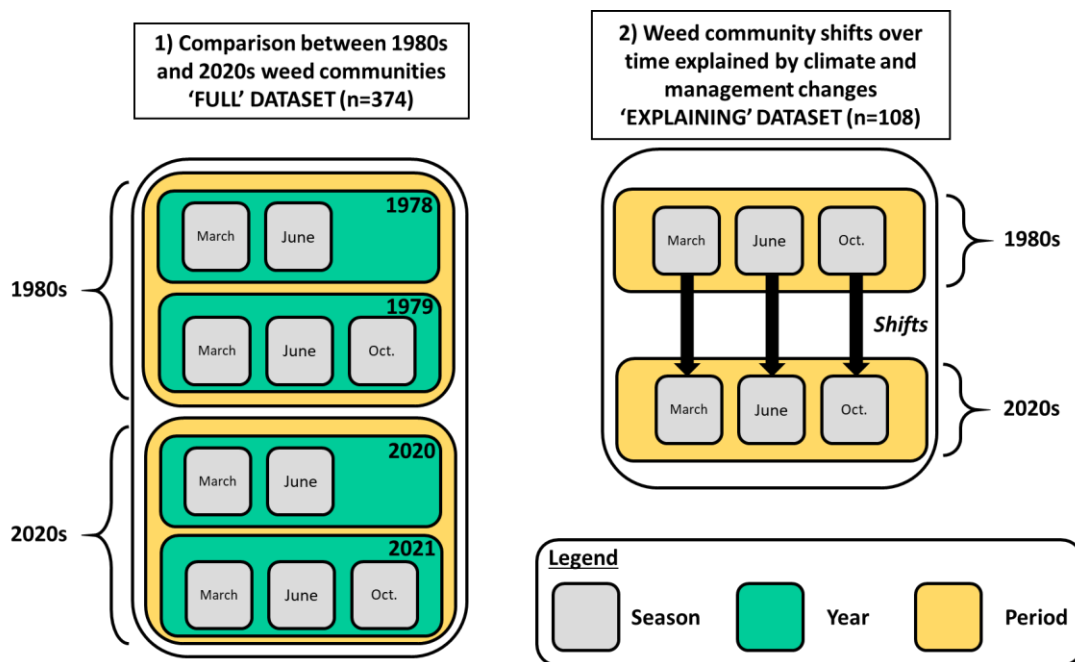


Figure 3 Two different datasets used for data analyses. The first one is the ‘full dataset’ composed of 374 floristic surveys from 1980s and 2020s, with all seasons (March, June, Oct. ; October) and years (1978, 1979, 2020, 2021). The second dataset is the ‘explaining dataset’ composed of 108 weed community shifts of the same seasons from the 1980s to 2020s

Table 1 Description of the metrics used to evaluate the shifts in climate, weed management, functional and taxonomic structure of the weed communities.

Type of drivers	Variable description	Computed metric
Climate change intensity	Relative change in the annual temperature range	$\Delta T^{\circ}C = \frac{T^{\circ}C\ range_{2020's} - T^{\circ}C\ range_{1980's}}{T^{\circ}C\ range_{2020's} + T^{\circ}C\ range_{1980's}}$ <p>With <math>T^{\circ}C\ range</math> which is the difference between the warmest month's and the coldest month's mean temperature</p>
Weed management trajectory from the 1980s to the 2020s	<p>The number of decades since the application of herbicides was stopped</p> <p>The number of decades since mowing was adopted</p> <p>The additional number of different management practices applied at the vineyard level from the 1980s to the 2020s, as a <i>proxy</i> of the trajectory toward more integrated weed management (<i>e.g.</i> if tillage was the only management practice used in the 1980s and if mowing and tillage were used in the 2020s, the value would be '1' additional weed management practice applied)</p>	

2020s weed management		The categorical variable of 4 groups of vineyards sharing the same 2020s weed management: <b>'Chem'</b> : vineyards with chemical weeding of both rows and inter-rows (n=4) <b>'Till.IR.Chem.R'</b> : vineyards with tilled inter-rows and chemically weeded rows (n=19) <b>'Mow.IR.Till.R'</b> : vineyards with mowed inter-rows and tilled rows (n=11) <b>'Till'</b> : vineyards with tilled rows and inter-rows (n=6)	
Functional differences between the 1980s and the 2020s weed communities	The shift in Community Weighted Means of traits	Specific leaf area (SLA), seed mass, maximum height, leaf Dry Matter Content (LDMC), lateral spread, flowering onset, duration of flowering, Ellenberg indices of temperature, light, nitrogen and soil moisture, % of C4	$\Delta CWM = \frac{CWM_{2020's} - CWM_{1980's}}{CWM_{2020's} + CWM_{1980's}}$
	The shift in CSR strategies	C, S and R scores	$\Delta Score = \frac{Score_{2020's} - Score_{1980's}}{Score_{2020's} + Score_{1980's}}$
	Shift along the functional space	<b>First dimension driven by phenology (Dim1)</b> From earlier and longer flowering to later and shorter flowering communities <b>Second dimension driven by soil moisture (EIV_F) and temperature requirements (EIV_T) (Dim2)</b> From low soil moisture and high-temperature requirements to high soil moisture and low-temperature requirements <b>Third dimension driven by photosynthetic pathways (Dim3)</b> From communities dominated by C3 species to communities dominated by C4 species  <b>Fourth dimension driven by SLA (Dim4)</b>	$\Delta CWM1 = Dim1_{2020's} - Dim1_{1980's}$ With Dim1, the coordinates of communities along the first axis of the CWM PCA $\Delta CWM2 = Dim2_{2020's} - Dim2_{1980's}$ With Dim2, the coordinates of communities along the second axis of the CWM PCA  $\Delta CWM3 = Dim3_{2020's} - Dim3_{1980's}$ With Dim3, the coordinates of communities along the third axis of the CWM PCA  $\Delta CWM4 = Dim4_{2020's} - Dim4_{1980's}$

With Dim4, the coordinates of communities  
along the fourth axis of the CWM PCA

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Taxonomic differences between the 1980s and the 2020s	Abundance, richness, Shannon and Pielou indices
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$$\Delta Index = \frac{Index_{2020's} - Index_{1980's}}{Index_{2020's} + Index_{1980's}}$$

# RESULTS

## 1. Climate and management changes from the 1980s to the 2020s

### 1.1. Climate change from the 1980s to the 2020s nearby Montpellier, France: the annual range of temperature increased by 1.2°C

Over the two periods, seasonal climate variables (spring, summer, autumn, winter temperatures, spring, summer, autumn, winter rainfall, and the annual number of frost days) of the vineyards were well explained by the first two PCA axes (84.7% of total variance) (Figure 4).

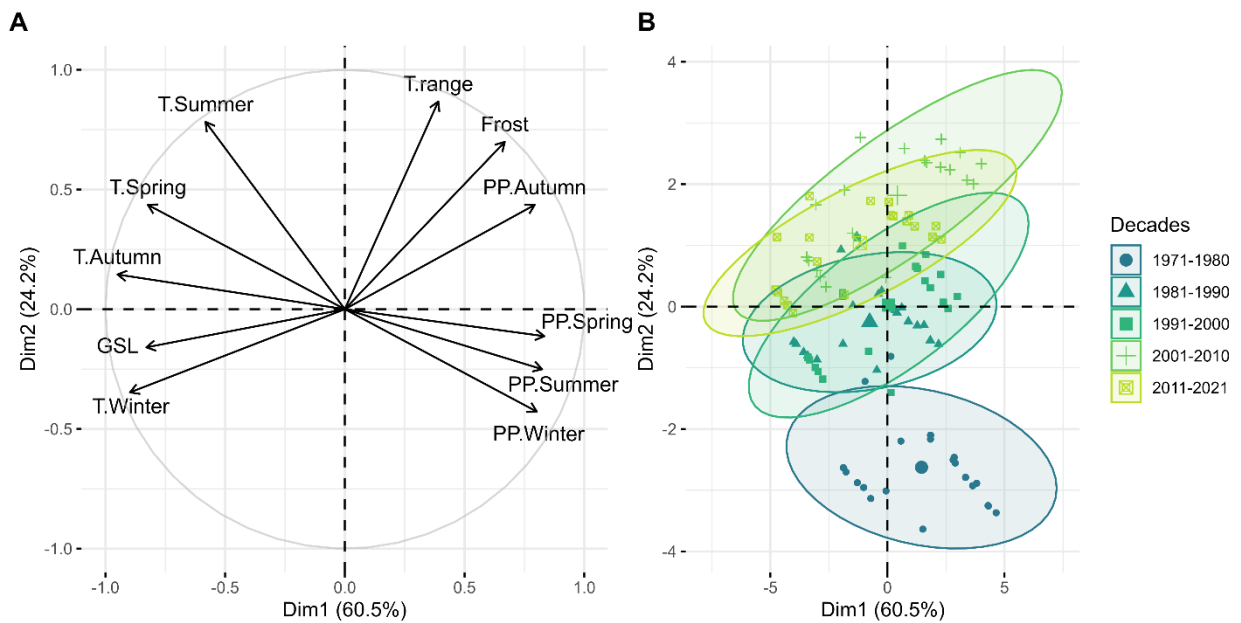


Figure 4 Climate change from the 1970s to the 2020s. **A)** Correlation circle of the climate variables on the first two axes of the climate PCA over the decades from the 1970s to the 2020s. **B)** Vineyard projection on the first two axes of the climate PCA for each decade from the 1970s to the 2020s. Each variable was averaged over the five studied decades: 1971-1980, 1981-1990, 1991-2000, 2001-2010, 2011-2021. T.Summer, mean summer temperature (°C); T.Spring, mean spring temperature (°C); T.Autumn, mean autumn temperature (°C); T.Winter, mean winter temperature (°C); PP.Spring, winter cumulated rainfall (mm); PP.Autumn, autumn cumulated rainfall (mm); PP.Winter, winter cumulated rainfall (mm); PP.Summer, summer cumulated rainfall (mm); T.range, annual temperature range (°C); Frost, number of frost days, GSL, growing season length.

The first axis explained most of the climate variance (60.5%) and intra-network variations across the vineyards from the same decades. This axis opposed vineyards located in warmer and drier areas with longer growing season length, located near the coastline to vineyards located in areas with higher rainfall, higher numbers of frost days and shorter growing season length, located in the northeast of the network. This axis also represented a slight decrease in seasonal precipitations over the decades (Figure S2). The second axis described mostly inter-decades variations of the climate conditions (24.2% of explained variance) (Figure 4, Figure S2). This axis was mainly driven by the annual range of temperatures (*i.e.* the difference between the warmest month's and the coldest month's mean temperatures), the summer temperature and the number of frost days. In 40 years, the annual range of temperatures increased by 1.2°C (from 13.5°C averaged over the 1971-1980 decade to 14.7°C averaged over the 2011-2021 decade). Moreover, summer temperatures have increased by 2°C in 40 years (21°C in the 1980s and 23°C in the 2020s) and spring temperatures by 1.4°C (12°C in the 1980s to 13.4°C in the 2020s) (Table 1). The annual number of frost days doubled in 40 years: from 11 days in the 1980s to 23 in 2020s (Table 1). Within the vineyard network, the increase in the annual range of temperatures was heterogeneous and varied from an increase of 0.9°C (vineyards located nearby the Mediterranean Sea) to an increase of 2.1°C (Northern vineyards) (Figure 2).

Table 2 Averaged climate and weed management characteristics in the 1980s and 2020s. Minimum and maximum values are reported in brackets.

Drivers	Variables	Unit	1980s	2020s
Climate	Annual temperature range	°C	15.7 (15-16.9)	17.4 (16.2-18.1)
	Growing season length	days	339 (328-353)	354 (337-363)
	Number of frost days	days	11 (5-16)	23 (6-38)
	Winter rainfall	mm	312 (232-373)	144 (98-179)
	Spring rainfall	mm	228 (169-273)	207 (128-254)
	Summer rainfall	mm	125 (84-151)	104 (71-127)
	Autumn rainfall	mm	265 (166-337)	293 (187-362)
	Winter temperature	°C	7.1 (5.9-8.2)	7.4 (6-8.8)
	Spring temperature	°C	12.0 (10.8-12.9)	13.4 (12.2-14.5)
	Summer temperature	°C	21.0 (19.9-22.1)	23.1 (22.1-24.2)
	Autumn temperature	°C	13.8 (12.6-14.8)	15.2 (13.8-16.5)
Management	Chemically weeded inter-rows	% of vineyards	35	22
	Tilled inter-rows	% of vineyards	63	95
	Mowed inter-rows	% of vineyards	0	78
	Chemically weeded rows	% of vineyards	70	68
	Tilled rows	% of vineyards	23	60

### 1.2. Weed practice shifts in 40 years in Mediterranean vineyards: mowing adoption from the 2000s

The first two axes of the PCoA based on the weed management practice variables of decades from the 1980s to the 2020s explained 72.2% of the total variance (Figure 5). The first axis opposed weed management practices from chemical weeding of rows ( $\rho$ : -0.69,  $P < 0.001$ ) and inter-rows ( $\rho$ : -0.77,  $P < 0.001$ ) to tillage of rows ( $\rho$ : 0.80,  $P < 0.001$ ) and inter-rows ( $\rho$ : 0.64,  $P < 0.001$ ) and mowing of inter-rows ( $\rho$ : 0.48,  $P < 0.001$ ). The second axis discriminated the vineyards with low numbers of weed management practices used at the plot level (one or two) from the ones with more integrated weed management (e.g. three different weed management practices applied at the plot level) (Figure 5).



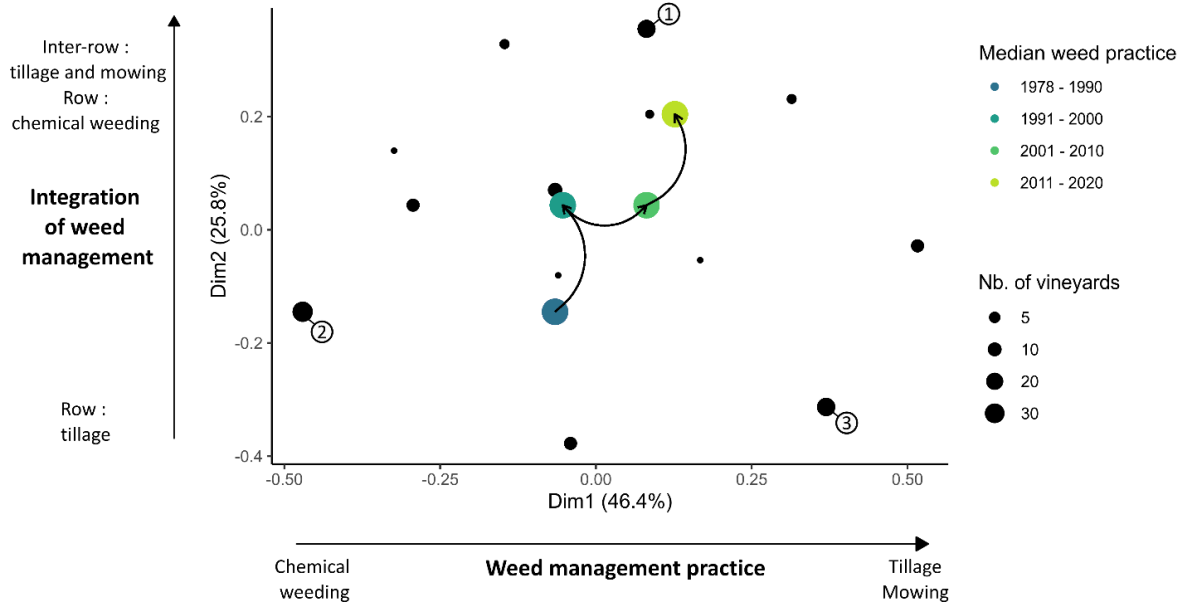


Figure 5 Changes in weed management practices from the 1980s to the 2020s in the PCoA space. Each dot represents a combination of weed practices at the plot level. The size of the black dots is proportional to the number of vineyards that share the same practice combination. The large coloured dots represent the median position of the vineyards of each decade in the PCoA space. The arrows illustrate the weed practice trajectory from the 1980s to the 2020s at the vineyard network scale. The first axis represents the weed management type used by the farmers. The second axis represents the number of weed practice types applied at the vineyard scale: from one practice type used (tillage of rows) to three practice types (tillage and mowing of inter-rows combined with chemically weeded rows). The vineyards located on position (1) in the practice PCoA are characterised by tillage and mowing of inter-rows and chemical weeding of the rows; the vineyards located on position (2) had chemically weeded rows and inter-rows ; the vineyards located in position (3) have rows and inter-rows that are tilled. Nb. of vineyards, number of vineyards sharing the same weed management practices.

More precisely, this axis opposed vineyards with tilled rows ( $\rho: -0.32, P < 0.001$ ) and either chemical weeding or tillage of inter-rows to vineyards with mixed combination of tilled ( $\rho: 0.51, P < 0.001$ ) and mowed inter-rows ( $\rho: 0.69, P < 0.001$ ) and chemical weeding of rows ( $\rho: 0.66, P < 0.001$ ). In the 1980s, farmers mostly tilled and applied herbicides. Mowing practice appeared in the 2000s, diversifying and increasing the number of weed management practices applied at the vineyard level. The median weed management practice that farmers applied in the 2020s was inter-row tilling and mowing and chemical weeding of rows (Figure 5). Thus, at the vineyard network level, the weed management shift from the 1980s to the 2020s was characterised by (i) less use of

chemical weed control on the inter-rows and (ii) a combination of more weed management practices at the plot level due to the adoption of mowing from the 2000s (Figure 5).

## **2. Shifts in weed community structure from the 1980s to the 2020s**

### *2.1. The diversity and the abundance of weed communities was higher in 2020s compared to the 1980s*

In total, 436 species were found over the 374 floristic surveys of the two periods. At the vineyard network scale, a similar number of species were identified 40 years apart: 320 species in the 1980s and 319 species in the 2020s. At the vineyard scale, the mean species richness was higher in the 2020s (34 species/community) than in the 1980s (26 species/community) (Figure 6). Community density showed the same trend that species richness: 68 individual plant/m<sup>2</sup> were found in the 2020s while 40 individual plant/m<sup>2</sup> were found in the 1980s. However, Shannon diversity was not significantly different between the two periods (2.39 in the 2020s and 2.40 in the 1980s) and the Pielou index was significantly lower in the 2020s (0.69 in the 2020s and 0.78 in the 1980s), demonstrating that the 2020s community were less equitable in abundance.

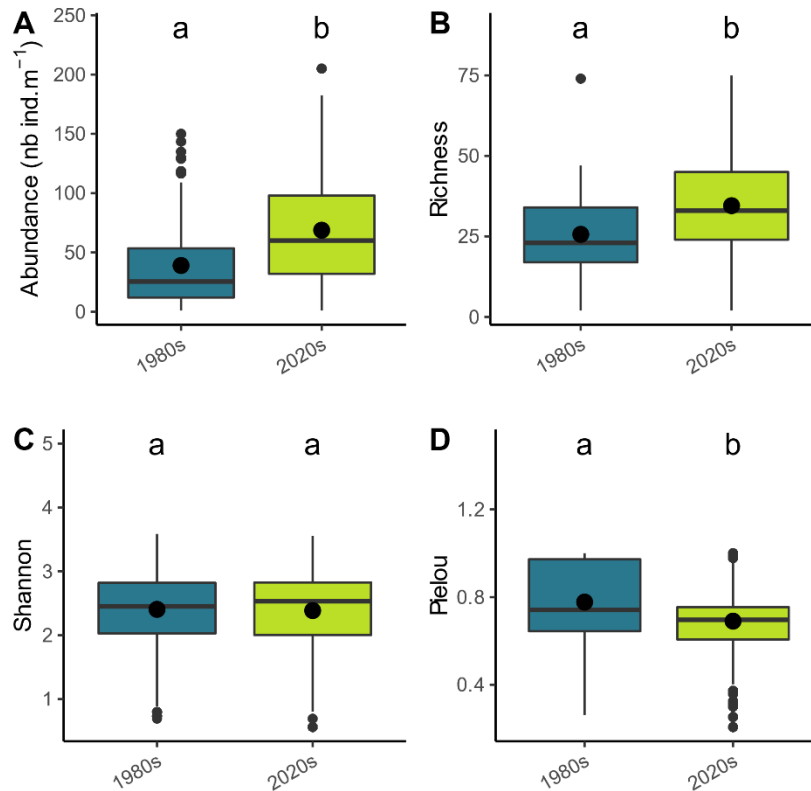


Figure 6 Differences in abundance (A), richness (B), Shannon indice (C) and Pielou indice (D) between the 1980s and the 2020s. Different letters indicate a significant difference in diversity indices between the two periods (Tukey's test with  $\alpha = 0.05$ ).  $n = 384$  floristic surveys

## 2.2. Therophytes are more frequent in the 2020s than in the 1980s weed communities

Current weed communities were composed of more therophytes compared to the 1980s communities (57% of the species in the 1980s compared to 80% in the 2020s) (Figure S3). In contrast, the 1980s communities were composed of more bulb geophytes (7% in the 1980s versus 1% in the 2020s), more rhizome geophytes (10% in the 1980s versus 4% in the 2020s), more biennial hemicryptophytes (7% in the 1980s versus 5% in the 2020s), more cespitose and erected hemicryptophytes (8% in the 1980s and 6% in the 2020s) and more hemicryptophytes with stolons (9% in the 1980s versus 3% in the 2020s).

### 2.3. Most of the species increased in abundance and frequency in 40 years

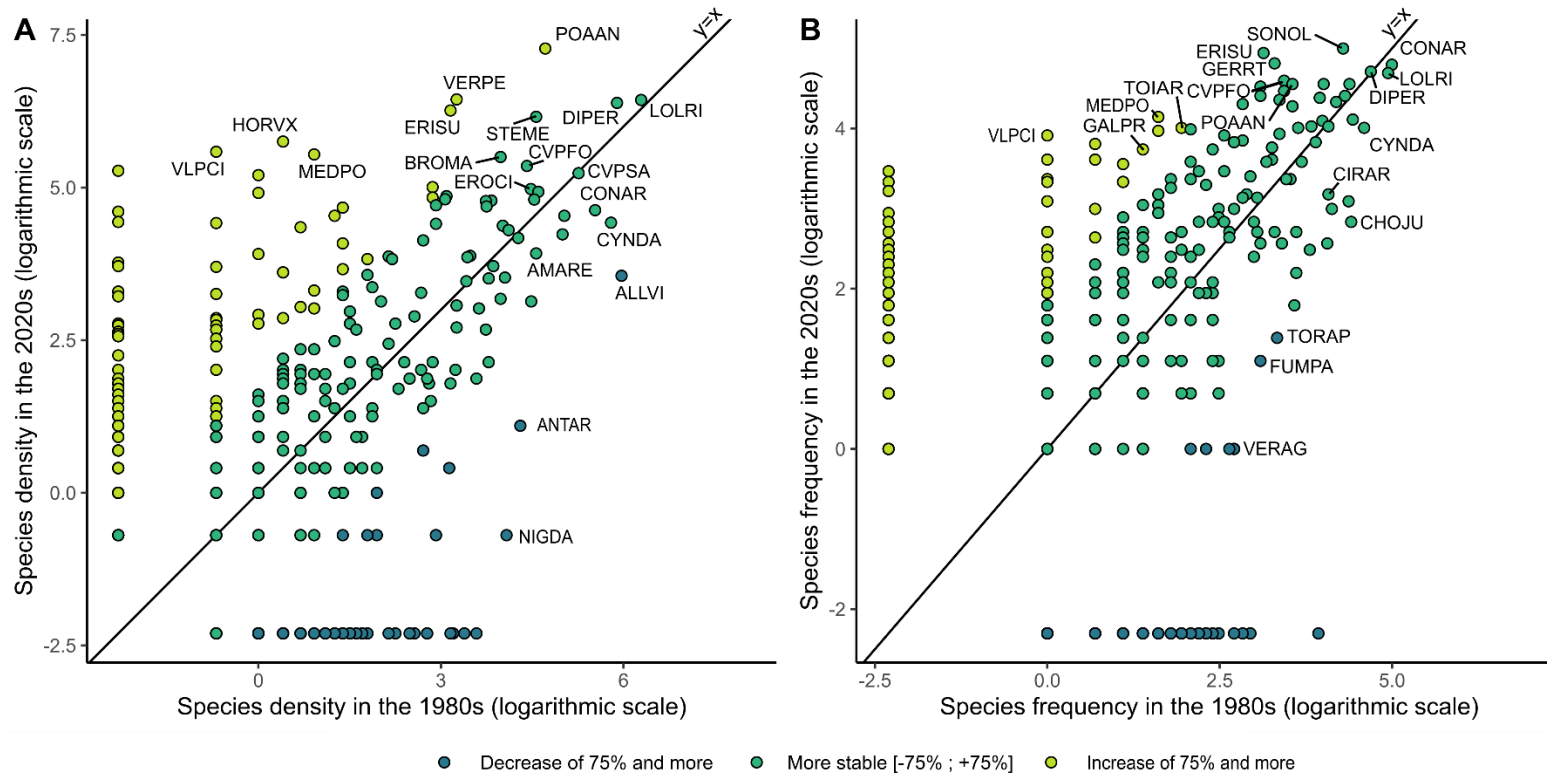


Figure 7 Changes in density (A) and frequency (B) for every 423 species that were found in the 1980s and/or in the 2020s. Each dot is a species and its colour describes to which extent its density and frequency have changed after four decades: dark blue dots represent species with density or frequency that decreased more than 75% from the 1980s to the 2020s; light green dots are the species with density or frequency that have increased by 75% or more; green dots are the more stable species. The dark line represents the  $y=x$  line. ALLVI, *Allium vineale*; AMARE, *Amaranthus retroflexus*; AN TAR, *Anthemis arvensis*; BROMA, *Anisantha madritensis*; CHOJU, *Chondrilla juncea*; CIRAR, *Cirsium arvense*; CONAR, *Convolvulus arvensis*; CVPFO, *Crepis foetida*; CVPSA, *Crepis sancta*; CYNDA, *Cynodon dactylon*; DIPER, *Diplotaxis eruroides*; ERISU, *Erigeron sumatrensis*; EROCI, *Erodium cicutarium*; FUMPA, *Fumaria parviflora*; GALPR, *Galium parisience*; GERRT, *Geranium rotundifolium*; HORVX, *Hordeum vulgare*; LOLRI, *Lolium rigidum*; MEDPO, *Medicago polymorpha*; NIGDA, *Nigella damascena*; POAAN, *Poa annua*; SONOL, *Sonchus oleraceus*; STEME, *Stellaria media*; TOIAR, *Torilis arvensis*; TORAP, *Tordylium apulum*; VERAG, *Veronica agrestis*; VERPE, *Veronica persica*; VLPCI, *Vulpia ciliata*.

Out of 423 species, 73 species had a strong decrease in abundance from the 1980s to the 2020s (more than 75%) while 116 species had a strong increase in abundance (more than 75%) (Figure 7, Supplementary data 2). Among the most abundant species in the 1980s and/or 2020s, the density of *Poa annua* (+86%), *Veronica persica* (+92%), *Erigeron sumatrensis* (+91%), *Vulpia ciliata* (+99%) and *Medicago polymorpha* (+98%) had strongly increased during the last 40 years. In contrast, the density of *Allium vineale* (-84%), *Cynodon dactylon* (-59%), *Cirsium arvense* (-59%), *Anthemis arvensis* (-92%) and *Nigella damascena* (-98%) had strongly decreased over time. *Lolium rigidum* (+7%) and *Crepis sancta* (-1%) were among the most stable and abundant species in abundance over time (Figure 7, Supplementary data 2).

One hundred and fourteen species had a strong decrease in frequency from the 1980s to the 2020s (more than 75%) while 135 species had a strong increase (more than +75%) (Figure 7, Supplementary data 3). Among the most frequent species in the 1980s and/or 2020s, the frequency of *Medicago polymorpha* (+85% of increase), *Torilis arvensis* (+77%), *Galium parisiense* (+83%) and *Vulpia ciliata* (+96%) increased strongly over time. In contrast, the frequency of *Tordylium apulum* (-75%), *Fumaria parviflora* (-76%) and *Veronica agrestis* (-88%) strongly decreased. *Lolium rigidum* (-12%) and *Diplotaxis eruroides* (+1%) were among the most stable and the most frequent species over time in the network (Figure 7, Supplementary data 3).

### **3. Shifts in weed community functional structure from the 1980s to the 2020s**

Community Weighted Means (CWM) of 13 traits were compared over the two periods (Figure 8). Eight CWM over 13 were significantly different over the two considered periods. Weed communities from the 2020s had significantly lower leaf area (937 mm<sup>2</sup> on average in the 1980s and 682 mm<sup>2</sup> on average in the 2020s), higher SLA (23.3 m<sup>2</sup>.kg<sup>-1</sup> on average in the 1980s and 25.0 m<sup>2</sup>.kg<sup>-1</sup> in the 2020s) and higher LDMC (181 mg.g<sup>-1</sup> in the 1980s and 198 mg.g<sup>-1</sup> in the 2020s) (Figure 8). They were also characterised by a higher duration of flowering (4.3 months in the 1980s and 5 months in the 2020s) and earlier flowering species (May on average in the 1980s and mid-April in the 2020s) compared to the 1980s communities. Moreover, the 2020s weed communities were

composed of species with lower seed mass (4.2 mg on average in the 1980s and 3.5 mg in the 2020s), lower lateral spread ability, lower water requirement, and lower proportion of C<sub>4</sub> species (11% in the 1980s and 5% in the 2020s).

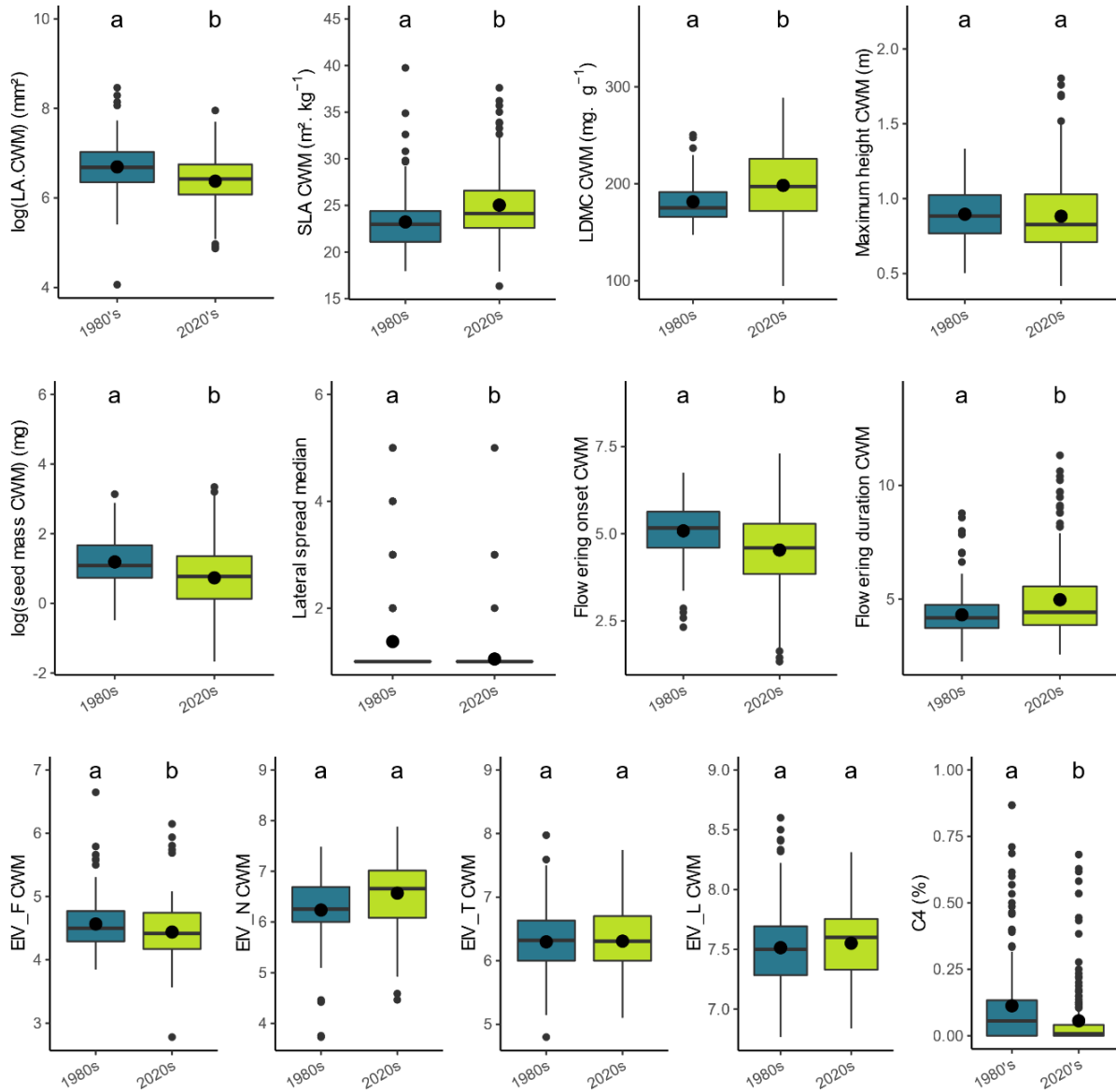


Figure 8 Community Weighted Means (CWM) changes in 40 years. Different letters indicate a significant difference of CWM between two periods. LA, Leaf Area ; SLA, Specific Leaf Area ; LDMC, Leaf Dry Matter Content ; Flow\_on.CWM, flowering onset ; Flow\_dur, duration of flowering ; EIV\_F.CWM, Ellenberg indice for soil moisture ; EIV\_T.CWM, Ellenberg indice for temperature ; EIV\_N.CWM, Ellenberg indice for nitrogen ; EIV\_L.CWM, Ellenberg indice for light.

Overall, weed communities of our Mediterranean vineyard network were mostly ruderal (54% of R-score on average) and competitive (31% of C-score on average) while they had 15% of Stress-tolerance-score (Figure 9). In 2020s, at the global community pool scale, the communities were less competitive (27% of C-score) than in the 1980s (34% of C-score) while they were more stress-tolerant (19% of S-score) than in the 1980s (12% of S-score) (Figure 9, Figure 10). The R-score was very stable over the two periods (54% for both periods).

Using the elbow inflexion point method on the AUC, the first four dimensions of the CWM space of the 1980s and the 2020s communities were selected (68.9% of total variance explained) (Figure S6). The first PCA axis explained most of the functional space variance (31.5%) and was driven by flowering phenology (Figure 11A, Table S1). This axis opposed late and short flowering communities to early and long-flowering communities (Figure 11A). Weed communities of the 2020s were dominated by earlier and longer flowering species compared to the 1980s communities (Figure 11B, C). The second PCA axis explained 14.2% of the variance of the functional space and described the community's environmental requirements. This axis was mainly driven by soil moisture and species temperature requirement (Figure 11A, Table S1). Weed communities from the 2020s were composed of species with lower soil moisture requirements and were more thermophilic compared to the 1980s communities (Figure 11B, D). The third axis of the functional space explained 10.5% of the variance and was mainly driven by the percentage of C<sub>4</sub> species within the communities (Figure S4A). 2020s weed communities were composed of more C<sub>4</sub> species compared to 1980s communities (Figure S4B, C). Finally, the fourth axis explained 10.2% of the functional variance at the community level and was mostly driven by SLA (Figure S4A, Table S1). This axis did not significantly discriminate the 1980s from the 2020s weed communities (Figure S4B, D). Many CWM correlated significantly (Table S2). Flowering onset was negatively correlated with the duration of flowering ( $\rho$ : -0.72,  $P < 0.001$ ) and positively correlated with maximum height ( $\rho$ : 0.75,  $P < 0.001$ ). The Ellenberg indices for temperature were positively related to Ellenberg indice for light ( $\rho$ : 0.64,  $P < 0.001$ ) (Table S2).

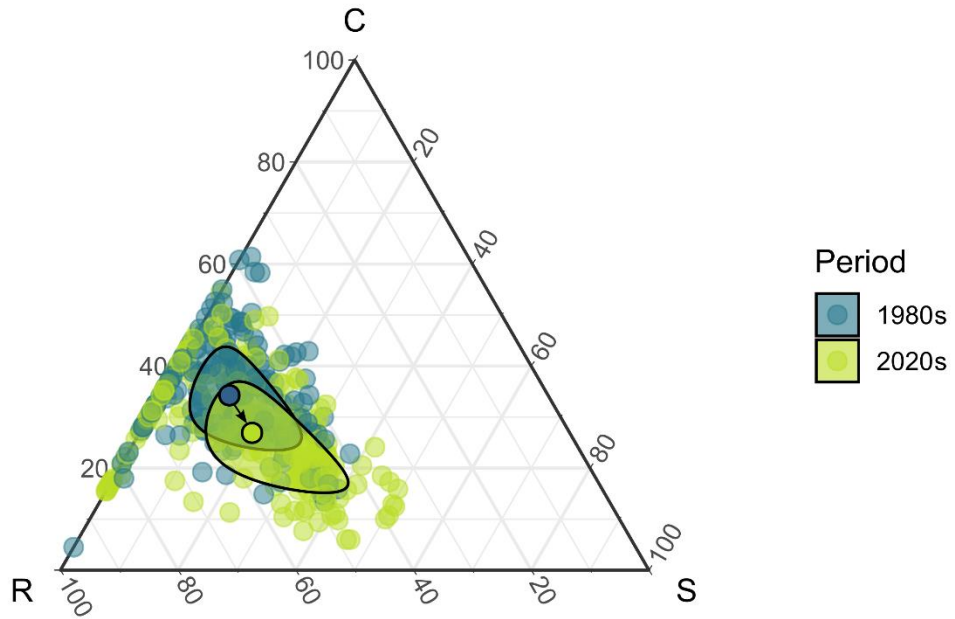


Figure 9 Shift in CSR strategies of weed communities from the 1980s to the 2020s in Grime's triangle. Each dot is a community and their color indicates the period when the community was observed (blue, 1980s ; light green, 2020s). The two dots with black outlines are the barycentres of the communities of each period and the black ellipses represent the variance of the CSR strategies of the communities from the two periods. The arrow represent the shift in the mean strategy from the 1980s to the 2020s. C, Competitors ; S, Stress tolerators ; R, Ruderal.

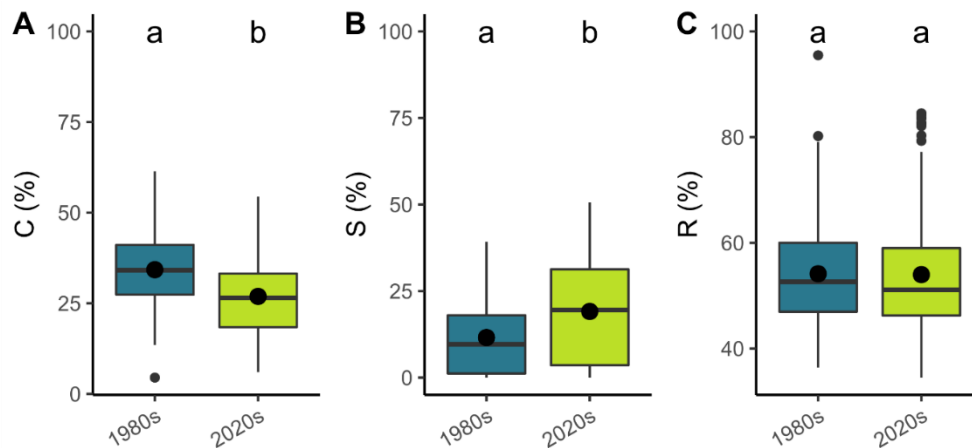


Figure 10 Difference of competitive (C), stress-tolerance (S) and ruderal (R) strategies of spontaneous vegetation communities over the periods.



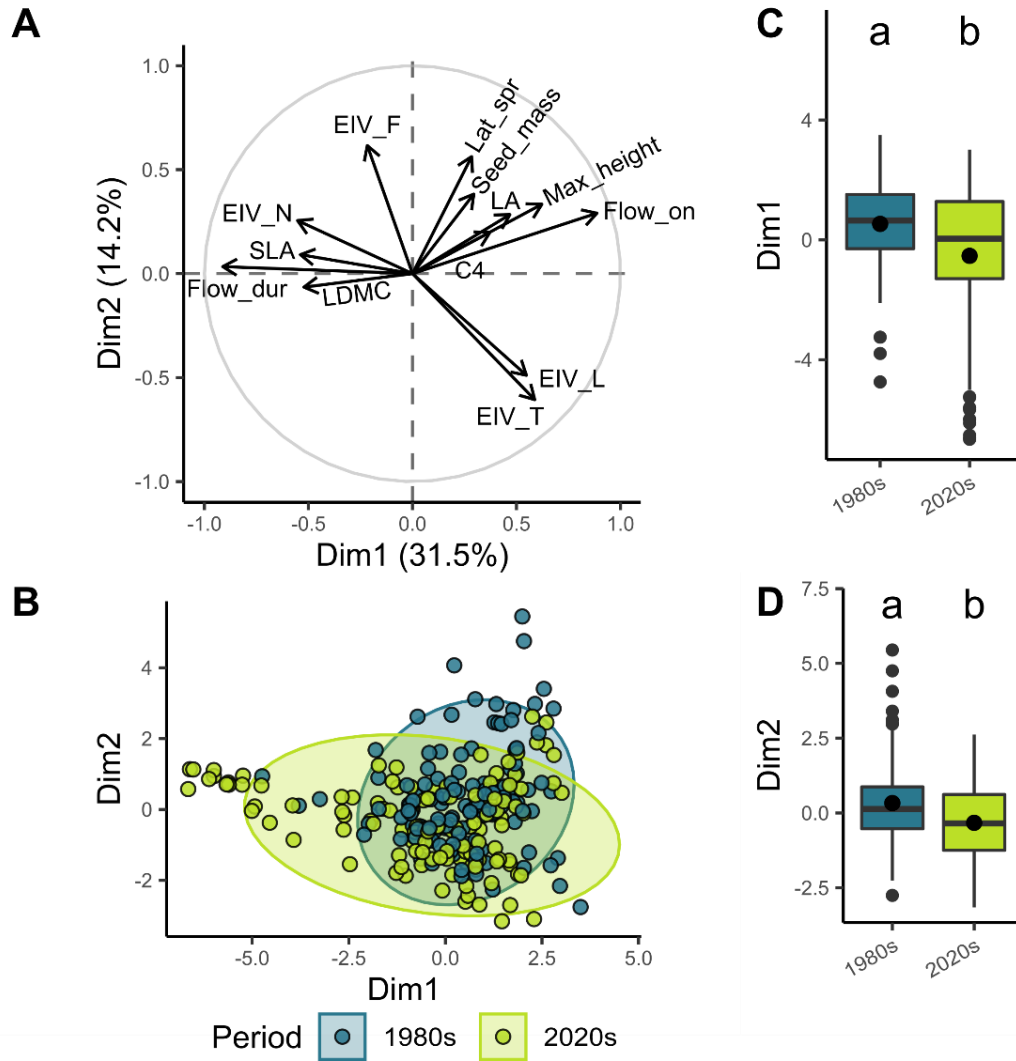


Figure 11 Functional shift in the weed communities from the 1980s to the 2020s along the first two axes of the PCA based on community weighted means (CWM). A) CWM constructing the first two axes of the functional PCA (A) are displayed in the correlation circles. B) The weed communities are projected on the first two dimensions. Each dot is a weed community and its colour refers to the period in which weed communities were observed: blue, 1980s ; green, 2020s. The significance of the differences in the coordinates of weed communities from the 1980s and the 2020s are presented for the first (C) and the second (D) dimensions of the functional PCA. Different letters indicate a significant difference in coordinates between the periods.

#### **4. Drivers of the shift in weed community functional and taxonomic structure between the 1980s and the 2020s**

##### *4.1. Neither climate change nor weed management explained the changes in abundance and diversity indices from the 1980s to the 2020s*

The following hypothesised drivers of weed community structure were tested as explaining factors of relative changes in abundance and in diversity (richness, Shannon and Pielou indices) from the 1980s to the 2020s: climate change (*i.e.* relative changes in annual temperature range), weed management trajectory from the 1980s to 2020s (temporality of herbicide application interruption and mowing adoption, and shift toward weed integrated management) and the 2020s weed management (2020s practices clusters: ‘Chem’, chemical weeding of both rows and inter-rows ; ‘Till.IR.Chem.R’, tilled inter-rows and chemically weeded rows ; ‘Mow.IR.Till.R’, mowed inter-rows and tilled rows ; ‘Till’, tilled rows and inter-rows). The relative change in the annual temperature range varied from 0.03 to 0.06 (averaged at 0.05). The number of decades since the application of herbicides was stopped ranged from 0 to 4 decades (averaged at 0.6) while the number of decades since mowing was adopted ranged from 0 to 3 (averaged at 1.7). The additional number of different management practices applied at the plot level from the 1980s to the 2020’s ranged from 0 to 2 (averaged at 1.2). However, none of these explaining variables was selected in the final models. Most of the variance was explained by the vineyard identity and season random effects: 31% for the changes in abundance, 61% for the changes in richness, 27% for the Shannon index and 9% for the Pielou index.

#### 4.2. *The drivers of the shifts in the functional properties of spontaneous vegetation communities between the 1980s and the 2020s*

Climate change, the weed management trajectory from 1980s to 2020s and the 2020s weed management practices classified into four groups (Chem, Till, Till.IR.Chem.R, Mow.IR.Till.R) were tested as explaining variables of CWM relative changes between the 1980s and the 2020s of the 13 traits. Vineyards that have experienced a higher climate change intensity from the 1980s to the 2020s (*i.e.* vineyards located in the northern part of the vineyard network, Figure 2) had more shifted to higher LDMC weighted means than vineyards that experienced climate change to a lesser extent (*i.e.* vineyards located nearby the Mediterranean Sea, Figure 2) (Table 2). Vineyards where chemical weeding was stopped for a long time, were composed of weed communities that had higher seed mass in the 2020s compared to the 1980s (Table 2, Figure 12). Weed communities that were continuously sprayed with herbicides during the four decades had shifted toward lower CWM of seed mass (-31% on average Figure 12). Vineyards that were managed toward more integrated weed management (*e.g.* vineyards managed entirely with tillage in the 1980s to vineyards management with mowing, tillage and chemical weeding in the 2020s) were composed of more C<sub>4</sub> species in the 2020s than in the 1980s. For the other CWM, the fixed effects were not selected in the final models, after model selection (Table S3, Table S4, Table S5).

The more intensive climate change (*i.e.* the higher relative change in annual temperature range over the periods), the higher shift in communities toward stress-tolerance strategies and away from ruderal strategies (Table 2). The shifts toward less competitive communities in the 2020s were explained by the adoption of integrative weed management practices: vineyards that were always managed by one type of weed management practice (tillage or chemical weeding) had less shifted toward a lower score of competitive strategies compared to vineyards where farmers adopted one or two other types of weed management practices.

Table 3 Standardised estimated coefficients of the explaining variables of the relative changes in community weighted means (CWM) and CSR strategies from the 1980s and the 2020s (C, Competitor ; S, Stress-tolerators ; R, Ruderal). Significant p-values ( $P < 0.05$ ) are in bold. Std. est. ; standardised estimates ; Std. err., standardised errors ; t, t-value ; P, p-value.

	<b>Explaining variables</b>	<b>Std. est.</b>	<b>Std. err.</b>	<b>t</b>	<b>P</b>	<b>Marginal R<sup>2</sup> / Conditional R<sup>2</sup></b>
<b>ΔCWM</b>						
<b>ΔSeed mass</b>	The number of decades since the application of herbicides was stopped	0.45	0.12	3.82	<b>&lt;0.001</b>	0.20 / 0.52
<b>ΔLDMC</b>	Relative changes in the annual T°C range	0.46	0.11	4.26	<b>&lt;0.001</b>	0.20 / 0.53
<b>ΔC4</b>	The shift toward integrated weed management (the additional number of different management practices applied at the vineyard level from the 1980s to the 2020s)	0.23	0.10	2.31	<b>0.023</b>	0.05 / 0.38
<b>ΔCSR strategy</b>						
<b>ΔC</b>	The shift toward integrated weed management (the additional number of different management practices applied at the vineyard level from the 1980s to the 2020s)	- 0.20	0.10	- 2.11	<b>0.037</b>	0.04 / 0.349
<b>ΔS</b>	Relative changes in the annual T°C range	0.46	0.10	4.71	<b>&lt;0.001</b>	0.21 / 0.42
<b>ΔR</b>	Relative changes in the annual T°C range	- 0.50	0.11	- 4.33	<b>&lt;0.001</b>	0.24 / 0.56

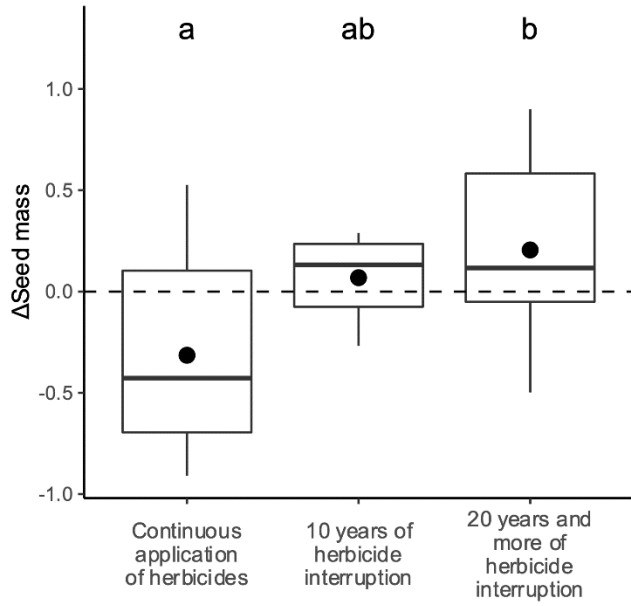


Figure 12 Seed mass shift according to the timing of herbicide interruption.  $\Delta\text{Seed mass}$  is equal to  $(\text{Community weighted seed mass}_{2020s} - \text{Community weighted seed mass}_{1980s}) / (\text{Community weighted seed mass}_{2020s} + \text{Community weighted seed mass}_{1980s})$

# DISCUSSION

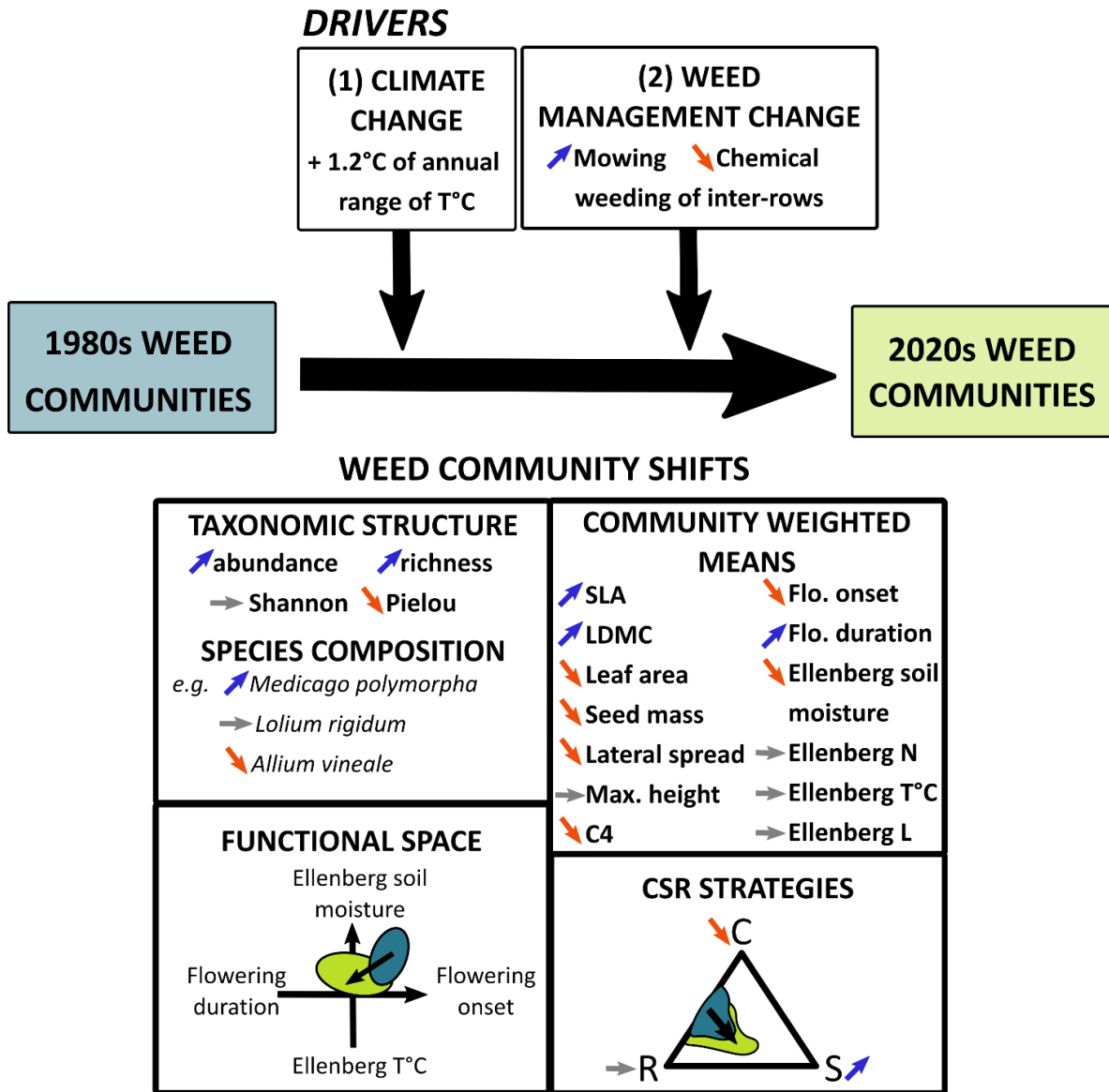


Figure 13 Summary of the main findings of this study. First, we demonstrated that climate change occurred during the four decades of the study time scale through the increase of the annual range of temperatures. Second, we found that weed management shifts from the 1980s to the 2020s were mostly characterised by the adoption of mowing and the ending of chemically weeding of the inter-rows. Third, we described major shifts in weed community: (i) higher abundance and richness and lower evenness, (ii) many species increased in abundance and frequency (e.g. *Medicago polymorpha*) while fewer decreased (e.g. *Allium vineale*) and others remain very stable (e.g. *Lolium rigidum*), (iii) community weighted means (CWM) of SLA, LDMC and flowering duration increased, while CWM of leaf area, seed mass, lateral spread, flowering onset, Ellenberg indice of soil moisture and the proportion of C4 decreased, (iv) weed communities shifted toward later and longer flowering, lower Ellenberg indice of soil moisture and higher Ellenberg indice of temperature, (v) weed communities shifted toward more stress tolerance strategies and less competitive strategies. Orange arrows represent significant decrease of the variables, blue arrows represent significant increases and grey arrows represent non-significant changes.

## 1. Significant changes in climate and weed management practices over four decades

We expected that climate change would be significant in the time scale of our study (four decades). Indeed, climate shifted from the 1980s to the 2020s toward a higher annual range of temperatures (*i.e.* the difference between the warmest month's and the coldest month's mean temperatures) that averaged around +1.2 °C (Figure 13). Seasonal temperature fluctuations of climate are expected to occur under climate change (Peters et al., 2014) and annual variability of temperatures was the best predictor of climate change in our dataset. Vineyards nearby the sea experienced a lower climate change intensity (+0.9°C of annual temperature range) than northern vineyards (+2.1°C). The buffering action of the sea and the two main drivers located all around the network (Hérault in the West and Vidourle in the East) could explain the lower intensity of climate change for vineyards located by the sea, in the Hérault plain and between Lunel and Quissac (Figure 2). In contrast with climate change projections (Fraga et al., 2020), growing season length (GSL) was not a significant driver of climate change. This was due to the climate gradient of the vineyard network, with high GSL in the southern vineyards and low in the northern vineyards. The doubling of the number of frost days from the 1980s to 2020s is in contrast with climate change projections (Meehl et al., 2004). While the studies of climate change in the Mediterranean area projected a decrease in precipitations (Tuel and Eltahir, 2020), seasonal precipitation variability over time explained fewer climate shifts than temperature metrics from the 1980s to the 2020s. Precipitation variability within the vineyards of the network was greater than its variability over time.

We hypothesised that weed management practices would strongly evolve toward less chemical weeding use and more tillage and mowing from the 1980s to the 2020s (Figure 13). Globally, weed management shifts matched our expectations and were driven by the adoption of mowing of the inter-rows that replaced chemical weeding of the inter-rows. More surprisingly, chemical weeding of rows and inter-rows was not widespread in 1978 and 1979 (*i.e.* the years of the first floristic surveys of this study) in the vineyard network. Indeed, 14 vineyards were managed using herbicides on both rows and inter-rows on 40 vineyards. Tillage of rows and inter-rows was still quite commonly applied (9/40 vineyards). Chemical weeding spread more widely in the decade

that followed the end of the 1970s, a few years after the first floristic surveys of this study. Maillet (1992) quantified for an extended network of vineyards around Montpellier (that included the vineyard network of this study) that 41% of vineyards shifted towards chemical weeding of both rows and inter-rows from 1979 to 1987. Moreover, in 1990s, the frequency of chemical weeding globally increased with a second application at the end of spring to control for summer species (Maillet, 1992). In our study, we did not consider the shift in frequency of weed management due to the difficulty of obtaining this data from farmers for the decades between 1980s and 2020s. Thus, if the median management that was used in the 1980s and in the 1990s is the same in our management trajectory characterisation, it is most likely that 1990s weed management were more intensive in herbicide use. We also did not explicitly consider in the characterisation of the weed management changes, the active ingredients of herbicides that were different between the two periods. In the 1980s, 95% of herbicides used were simazine (pre-emergence) and aminotriazole-based (post-emergence) and were applied mostly between February and April (Maillet, 1981). Only 8% of the 1980s farmers applied herbicides a second time to control perennials (*e.g. Convolvulus arvensis*). In the 2020s, herbicides were glyphosate-based (post-emergence herbicide) and applied once approximatively at the same period. If the spectrum of these herbicides from both periods was broad (*i.e.* targeting both annuals and perennials), persistence over time was different: simazine can persist from three months to 15 months while aminotriazole and glyphosate persist less than one month (Maillet, 1981). Thus, in 1980s, chemical weeding had a longer controlling action on weed communities. This could explain for instance, that the plots that were continuously chemically weeded between the 1980s and the 2020s showed a slight increase of species richness (13%). Moreover, even though this practice was not considered in the analysis because of too much missing data over time, irrigation of the rows tended to increase from the 1980s (only 2/40 vineyards equipped with irrigation systems) to the 2020s (9/40 vineyards). We also did not consider the evolution of fertilisation and amendment due to missing data.



## **2. Increase of richness, abundance and decrease of evenness overtime which were neither explained by weed management nor by climate change**

Weed communities from the 2020s were 41% more abundant and 24% more diverse in species than the 1980s communities at the vineyard level (Figure 13). In arable lands, previous studies on weed changes over time showed drastic opposite trends: -42% to -46% in species richness from the 1970s to 2000s (Fried et al., 2016, 2009b) and -67% in species density (Fried et al., 2009b). The contrast between these studies and our results can be explained by a different temporal coverage. The period 1970s-2000s captured the strong filtering effect of herbicide adoption in arable lands before changes in more extensive weed management practices in the 2000s (Fried et al., 2009a). On the contrary, the two decades from 2000s to 2020s captured the effect of the development of more agroecological weed management practices, especially in vineyards with the adoption of mowing to control 2020s weed communities.

If weed communities in the 2020s were richer in species and number of individuals (abundance), they were characterised by a lower evenness than four decades before. However, neither weed management practice trajectory, nor climate change explained the shift in species abundance, richness and evenness. Landscape-level factors that we did not consider in this study might explain these shifts. For instance, agricultural surface decreased by 28% in Hérault from 1970 to 2020 (Chambre d'agriculture de l'Hérault, 2021). Surface dedicated to vineyard cultivation also decreased in the proportion of the total agricultural area (from around 64% in 1970 to 39% in 2020) while grassland areas were quite stable over time (Chambre d'agriculture de l'Hérault, 2021). Moreover, forest cover increased strongly: from 22% of the area of Hérault in 1974 to 48% in 2017 (IGN, 2022). Thus, species coming from the forest, garrigue or grasslands might have colonised vineyards and increased species richness at the plot level.

If the shifts in richness and abundance were not explained by changes in weed management practices, previous studies demonstrated that some increaser and decreaser species in abundance were favoured by some weed management practices. For instance, *Erigeron sumatrensis* whose abundance increased by 91% from the 1980s to the 2020s has been recently reported to have glyphosate-resistant populations (Leal et al., 2022) as well as *Poa annua* (Baldwin et al., 2012) which

also increased by 87%. *Erigeron sumatrensis*, *Torilis arvensis* and *Galium parisiense* which abundance increased in our vineyard network were already increasing exponentially from 1979 to 1987 in chemically weeded vineyards of the extended network (Maillet, 1992). These selected species are the results of the two decades of intensive herbicide use (1980s to 1990s) and might still be favoured by chemical weeding of rows. The abundance of *Cirsium arvense* and *Allium vineale* decreased by 59% and 84% respectively at the community level in four decades. The frequency of *Allium vineale* and *Cirsium arvense* were also decreasing from 1979 to 1987 in the part of the extended network of vineyards that were controlled with herbicide continuously during this period (Maillet, 1992). A recent meta-analysis on *Cirsium arvense*'s management showed that herbicides were very efficient but that integrated weed management was even more effective for the long-term control of this species (Davis et al., 2018).

### **3. Climate change-induced weed community shifts toward more stress-tolerance**

According to our hypothesis, at the regional scale, weed communities shifted toward more stress tolerance (+37% of S-score) (Figure 13). Weed communities, that shifted toward a higher score of stress tolerance from the 1980s to the 2020's, have also experienced a higher intensity of climate change (*i.e.* higher increase of annual temperature range). To our knowledge, this study is the first to demonstrate that stress tolerance of weed communities is increasing in response to climate change through changes in species composition. The shift toward a higher stress tolerance, driven by climate change did not result from a decrease of species with competitive strategies but rather from a decrease of ruderal strategies. Indeed, our results showed that both S and R-scores were driven by climate change intensity (S positively and R negatively). In contrast, the decrease in weed community C-score over time was induced by weed management.

The increase in stress tolerance is linked to the increase of the community level leaf dry matter content (181 mg.g<sup>-1</sup> in the 1980s and 198 mg.g<sup>-1</sup> in the 2020s) which is the *proxy* of stress tolerance in Pierce et al.'s algorithm (2017) (Figure 13). The increase in LDMC was also explained by

the increase in annual range temperature in the selected models. This indicates that climate change intensity reshuffled community composition toward more conservative species which invest in leaves with thicker and stiffer cell walls that can maintain turgidity at low water potential (Garnier et al., 2019). Other shifts of community-level traits indicated more conservative and stress tolerance communities even though they were not significantly linked to the intensity of climate change. For instance, leaf area decreased over time which has been related to a drought-tolerance strategy (de la Riva et al., 2018). Ellenberg's indice of soil moisture of weed communities also decreased significantly. Weed communities had earlier and longer flowering times in the 2020s compared to the 1980s which could also be explained by a longer growing season (Menzel et al., 2006). Surprisingly, the proportion of C<sub>4</sub> species within the weed communities decreased over time while it is expected that C<sub>4</sub> species would increase with climate change as their photosynthesis pathway is more efficient than those of C<sub>3</sub> at higher temperatures (Heilmeyer, 2019; Peters et al., 2014). However, independently of temperature and precipitation changes, the increasing level of CO<sub>2</sub>, that we did not consider in the way we defined climate change in our study, has been predicted to favour C<sub>3</sub> more than C<sub>4</sub> (Peters et al., 2014). Indeed, C<sub>3</sub> weeds increased more their leaf area and their biomass in higher CO<sub>2</sub> pressure than C<sub>4</sub> species. Thus, they are more competitive in such conditions. However, the driver of this C<sub>4</sub> decrease was linked to weed management as for the C-score decrease.

#### **4. The diversification of weed management practices over time favoured less competitive weed communities**

We hypothesised that the decrease of herbicide use replaced by tillage and mowing would favour more conservative and competitive strategies for two reasons. First, mowing is a lower intensity disturbance than chemical weeding and would filter more conservative strategies than other management practices. Second, weed biomass and competition for resource might be higher in mown communities, selecting competitive species. In contrast with our expectations, communities from the 2020s were less competitive than communities from the 1980s (34% of C-score in the 1980s versus 27% of C-scores in the 2020s) while mowing appeared in the 2000s (Figure 13). This

decrease in competitive ability was driven by the number of different weed management practices applied at the plot level. A shift toward a higher diversity of weed management practices and consequently more integrated management of weeds induced a higher decrease in C-score. C-score is proxied by leaf area in Pierce et al.'s algorithm (2017) which also decreased over time. The diversity of disturbance types, intensity and frequency of integrated managed vineyards favoured communities composed of species that did not invest in large leaf areas and high maximum height (which was positively correlated to leaf area in our study) and thus were less competitive to capture light. However, this contrasted with the higher SLA of weed communities from the 2020s compared to the 1980s (Figure 13). At the community level, SLA and LA were not significantly correlated. Even though the effect of integrated weed management on C-score was quite low (estimate: -0.20) and with a high  $p$ -value (0.037), these results demonstrate that weed management is a lever of action to filter more desirable weed communities that are less competitive with the main crops (MacLaren et al., 2020).

Weed communities that were sprayed with chemical weeding continuously for four decades shifted toward lower seed mass (on average, -31% of seed mass at the community level) while those where herbicides were interrupted for more than 20 years, showed the opposite trend (+22% of seed mass) (Figure 13). As seed mass is negatively correlated to seed number (Westoby, 1998), weed community strategies under chemical control is to produce a high number of seeds to face a higher risk of seed mortality (Storkey et al., 2010). Moreover, small seeds may have higher seed dormancy (Thompson et al., 1993) leading to a lower depletion of the seed bank. In tilled vineyards, seeds can be buried in the top 5 centimeters of the soil after tillage and are less exposed to desiccation. As heavier seeds are most likely to germinate when they are buried (Benvenuti et al., 2001), weed community strategy under tillage is to produce large seeds with a better probability of seedling establishment.

## 5. Future weed communities: a threat or an opportunity for vineyards ?

The trend toward more stress-tolerant, less competitive and more diverse weed communities contrasted with several studies in annual crops (Moss et al., 2004; Storkey et al., 2010). In annual cropping systems, the temporal increase in weed competitiveness was observed and was partly related to an increase of nitrogen input (Storkey et al., 2021). Fertilisation is a factor that we did not consider in our study management due to the difficulty of obtaining this data from farmers. However, fertilisation in vineyards is quite low (Metay et al., 2014) and the global temporal trend of fertilisation in vineyards contrasted with the trend in annual cropping systems. Indeed, vineyard fertilisation has decreased over the past decades in the aim of increasing wine quality (Verdenal et al., 2021) and this trend could also explain the decrease in weed community competitiveness. In this context, weed communities that are more stress tolerant with water-saving strategies and thus less water needs, as found in our study, are desirable to decrease weed-vine competition for water (MacLaren et al., 2020). The yield of Mediterranean vineyards is expected to decrease from 7 to 14% by 2100 due to climate change and some studies demonstrated that irrigation might not be sufficient to compensate this decrease (Fraga et al., 2018; Naulleau et al., 2022). Grape phenology is already earlier and wine quality is expected to decline (Neethling et al., 2019). Many reviews discussed the future of vineyards in a changing climate context with necessary adaptation at large scale (*e.g.* changes in geographical location of terroirs) (Neethling et al., 2019; Santillán et al., 2019) but also at the vineyard level (Fraga et al., 2012; Naulleau et al., 2022) accounting for both short-term climate variability and long-term changes. They pointed out that Mediterranean region would require the largest adaptation effort (Santillán et al., 2019). Weed management is a way for farmers to manage temporal variations in vine water supply which is a key determining factor of crop productivity and fruit quality (Van Leeuwen et al., 2009). Changes in weed management strategies (*e.g.* choice to sow a cover crop in the inter-rows) and weed management tactics (*e.g.* choice of the date of weed destruction) are both needed to adapt to higher temporal uncertainty, for short and long-term changes.

## **CONCLUSION**

The current trend of herbicide abandonment for tillage and mowing is driving weed communities to higher diversity, higher abundance and more uneven distribution in Mediterranean vineyards. In response to climate change, weed communities were more stress-tolerant, an optimal strategy to cope to future climate conditions. In this article, we demonstrated that weed communities are adapting to climate change and that weed management is a strong lever for action to model diverse and functional weed communities in the future.

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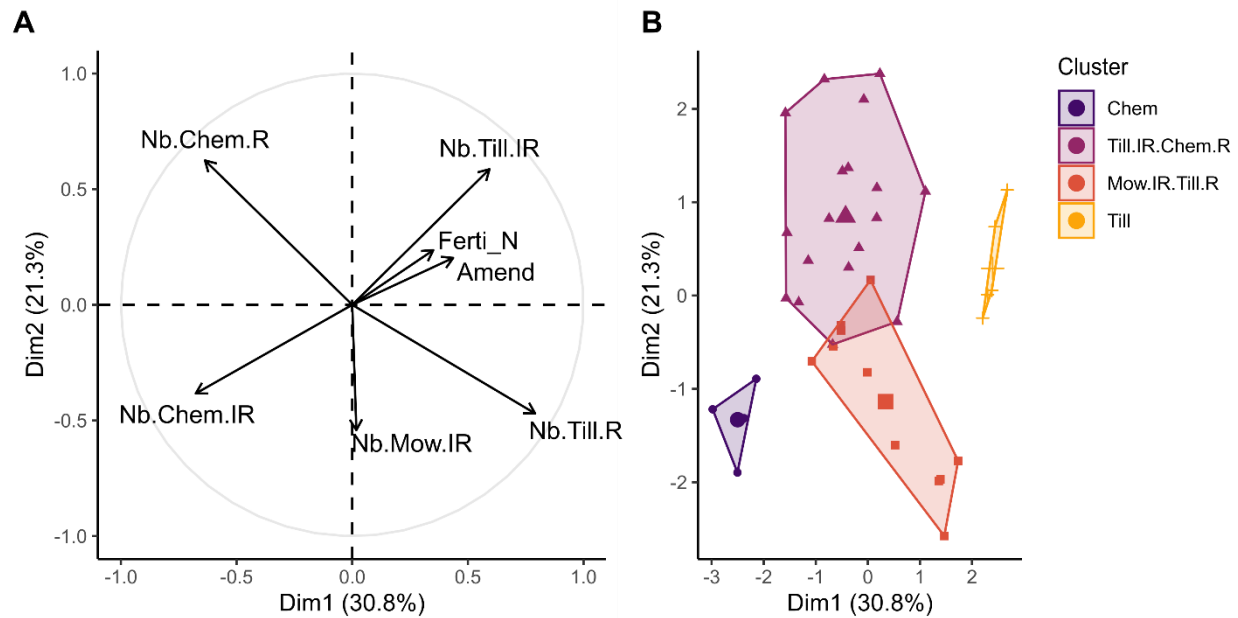
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## SUPPORTING FIGURES



*Figure S1A* Circle of correlation of the agricultural practices applied by the farmers from 2015 to 2021 projected on the first two axes of the PCA (Dim1, Dim2). Each practice variable is averaged over the 2015-2021 period. Nb.Chem.IR, number of chemical weeding sprayed in the inter-rows ; Nb.Chem.R, number of chemical weeding sprayed in the rows ; Nb.Till.IR, number of tillage of the inter-rows ; Nb.Till.R, number of tillage of the rows ; Nb.Mow.IR, number of mowing of the inter-rows ; Ferti\_N, nitrogen inputs ; Amend, soil amendment. **B** Clusters of vineyards sharing similar agricultural practices displayed on the first two axes of the PCA. Each dot is a vineyard and its colour indicates to which cluster it belongs. Vineyards were classified in four clusters. Cluster 'Chem' gathers four vineyards with chemical weeding of both rows and inter-rows. Cluster 'Till.IR.Chem.R' regroups 19 vineyards with tilled inter-rows and chemically weeded rows. Cluster 'Mow.IR.Till.R' gathers 11 vineyards with mowed inter-rows and tilled rows. Cluster 'Till' groups six vineyards with tilled rows and inter-rows.

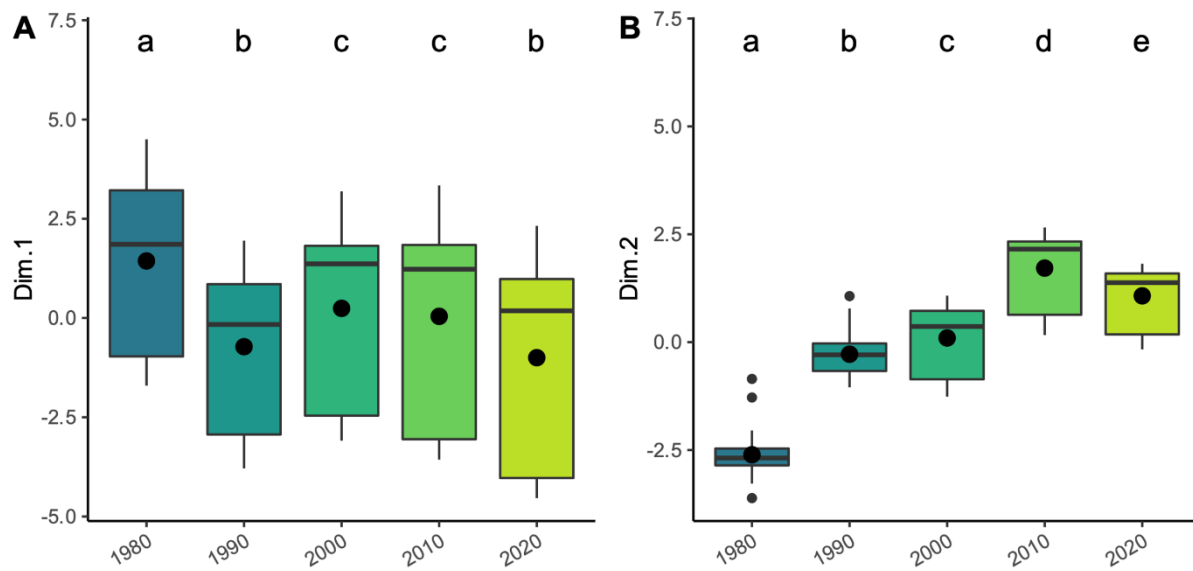


Figure S2 Coordinate changes of vineyards on the first axis (A) and the second axis (B) of the climate PCA over the decades from the 1980s to the 2020s. Different letters indicate a significant difference between decades.

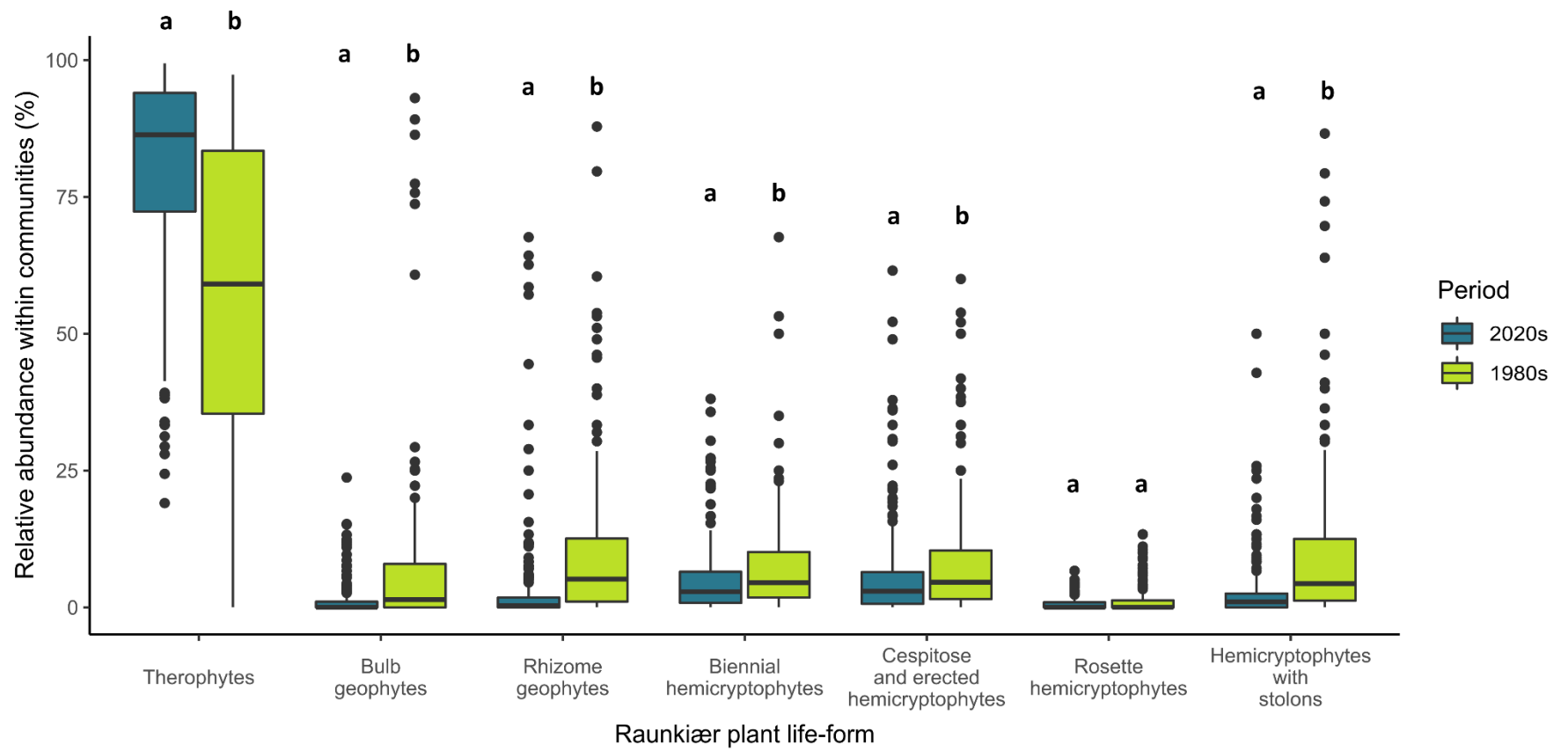


Figure S3 Relative abundance of Raunkiaer plant-life form within 1980s and 2020s weed communities.

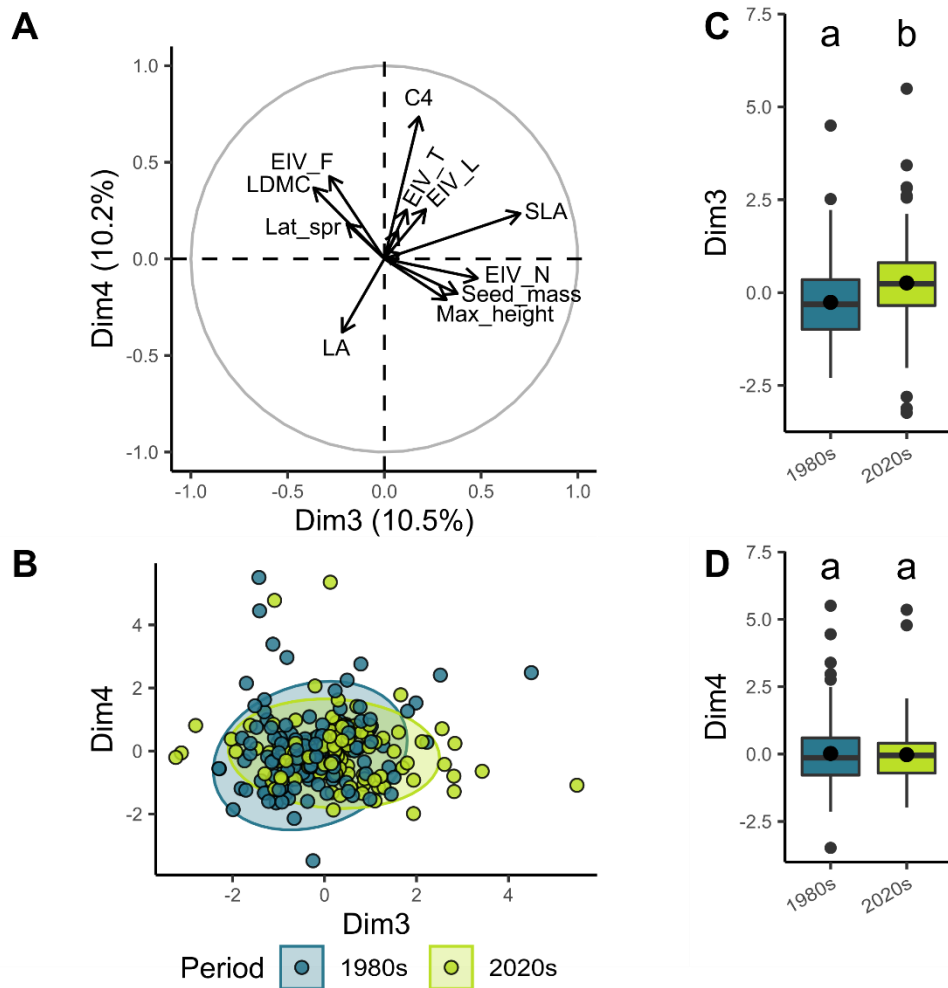


Figure S4 Functional shift in the weed communities from the 1980s to the 2020s along the third and fourth axes of the PCA based on community weighted means (CWM). A) CWM constructing the third and fourth axes of the functional PCA are displayed in the correlation circles. Poorly represented CWM were removed from the graph for reasons of readability (flowering onset and flowering duration). B) The weed communities are projected on the third and fourth axes. Each dot is a weed community and its colour refers to the period in which this community was observed: blue, 1980s ; green, 2020s. The significance of the differences in the coordinates of weed communities from the 1980s and the 2020s are presented for the third (C) and the fourth (D) dimensions of the functional PCA. Different letters indicate a significant difference in coordinates between the periods.

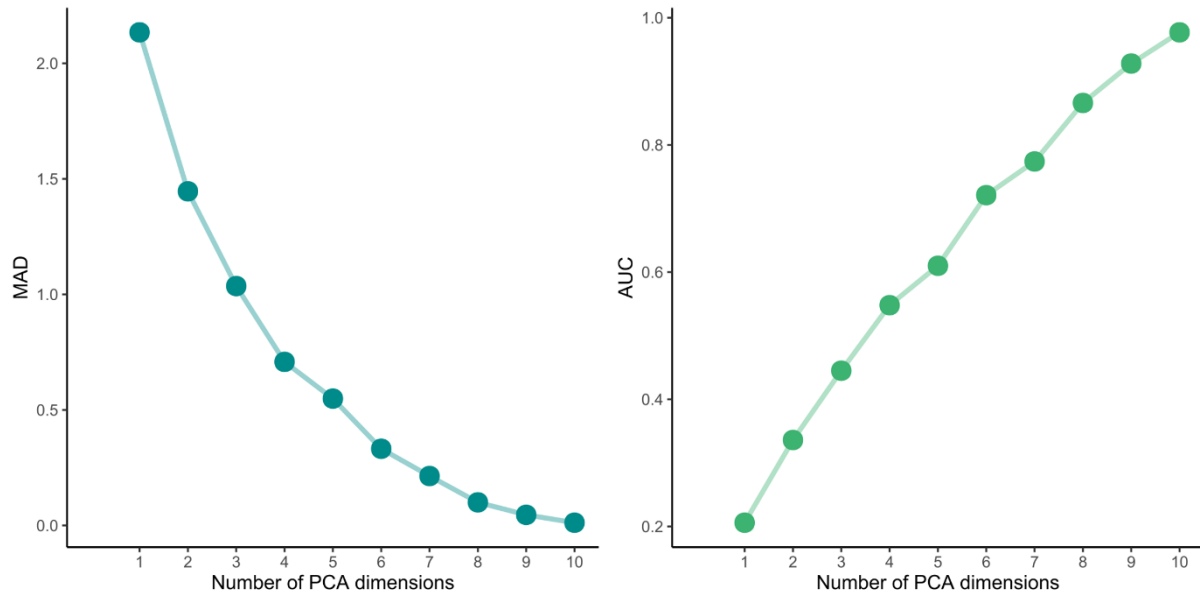


Figure S5 The quality of the community functional space according to the selected number of PCA dimensions: (i) the AUC (Area Under the Curve) based on the Somer's D statistic which measures the difference of ranking between the communities of the initial data set and the communities displayed in the PCA and (ii) the MAD (Mean Absolute Deviation) measures the Euclidean distance between communities' position in the initial data set and the PCA. Using the method of the elbow infection point method proposed by Mouillot et al. (2021) on AUC, we determined that four dimensions would be necessary to describe the functional space.



## SUPPORTING TABLES

*Table S1 Community Weighted Means contribution to the first four dimensions of the PCA of 1980s and 2020s communities (%). SLA, Specific Leaf Area ; LA, Leaf Area ; LDMC, Leaf Dry Matter Content ; Lat\_spr, Lateral spread ; EIV\_F, Ellenberg indice for soil moisture ; EIV\_T, Ellenberg indice for temperature ; EIV\_N, Ellenberg indice for nitrogen ; EIV\_L, Ellenberg indice for light; Flow\_on, flowering onset ; Flow\_dur, duration of flowering.*

	<b>Dim1 (%)</b>	<b>Dim2 (%)</b>	<b>Dim3 (%)</b>	<b>Dim4 (%)</b>
SLA	7	0	36	4
LA	5	4	3	11
LDMC	7	0	10	10
Seed_mass	2	8	10	2
Max_height	9	6	7	3
C4	3	2	2	41
Lat_spr	2	17	3	2
EIV_F	1	21	6	14
EIV_T	8	20	1	5
EIV_N	7	4	17	1
EIV_L	7	13	3	5
Flow_on	19	5	0	2
Flow_dur	20	0	0	0

Table S2 Pairwise correlations between functional metrics at the community level. The coefficients of significant correlations are reported in bold. *P*-values were corrected from multiple testing using Holm correction. *SLA*, Specific Leaf Area ; *LDMC*, Leaf Dry Matter Content ; *Lat\_spr*, Lateral spread ; *EIV\_F*, Ellenberg indice for soil moisture ; *EIV\_T*, Ellenberg indice for temperature ; *EIV\_N*, Ellenberg indice for nitrogen ; *EIV\_L*, Ellenberg indice for light ; *Flow\_on*, flowering onset ; *Flow\_dur*, duration of flowering ; *LA*, leaf area.

	LDMC	Seed_mass	EIV_F	EIV_T	EIV_N	EIV_L	Flow_on	Flow_dur	C4	Lat_spr	Max_height	LA
SLA	0,09	-0,15	0,06	<b>-0,18</b>	<b>0,35</b>	-0,09	<b>-0,25</b>	<b>0,42</b>	0,00	<b>-0,21</b>	<b>-0,20</b>	<b>-0,38</b>
LDMC	-	<b>-0,19</b>	<b>0,21</b>	-0,11	0,03	-0,07	<b>-0,34</b>	<b>0,22</b>	<b>-0,20</b>	-0,07	<b>-0,33</b>	<b>-0,31</b>
Seed_mass		-	-0,11	0,03	<b>-0,23</b>	0,00	<b>0,39</b>	<b>-0,34</b>	<b>0,21</b>	<b>0,26</b>	<b>0,38</b>	<b>0,32</b>
EIV_F			-	<b>-0,48</b>	<b>0,21</b>	<b>-0,30</b>	0,02	0,13	-0,01	<b>0,18</b>	-0,08	-0,05
EIV_T				-	<b>-0,30</b>	<b>0,64</b>	<b>0,20</b>	<b>-0,45</b>	<b>0,29</b>	-0,02	0,00	0,14
EIV_N					-	-0,14	<b>-0,34</b>	<b>0,27</b>	<b>-0,45</b>	-0,13	-0,07	<b>-0,24</b>
EIV_L						-	<b>0,33</b>	<b>-0,43</b>	<b>0,21</b>	-0,06	<b>0,27</b>	0,15
Flow_on							-	<b>-0,72</b>	<b>0,56</b>	<b>0,34</b>	<b>0,75</b>	<b>0,42</b>
Flow_dur								-	<b>-0,27</b>	<b>-0,29</b>	<b>-0,49</b>	<b>-0,40</b>
C4									-	<b>0,23</b>	<b>0,34</b>	<b>0,24</b>
Lat_spr										-	<b>0,23</b>	<b>0,27</b>
Max_height											-	<b>0,51</b>

Table S3 Selected fixed effects of the Community Weighted Mean relative differences in the 1980s and the 2020s. SLA, Specific Leaf Area.

	<b><math>\Delta</math>SLA</b>	<b><math>\Delta</math> Max_Height</b>	<b><math>\Delta</math> Lateral_spread</b>
<i>Selected predictors</i>	<i>No fixed effects selected</i>	<i>No fixed effects selected</i>	<i>No fixed effects selected</i>
Observations	108	108	108
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0 / 0.52	0 / 0.39	0 / 0.12

Table S4 Selected fixed effects of the Community Weighted Mean relative differences in the 1980s and the 2020s. *EIV\_L*, Ellenberg indice for light;  $\Delta.EIV_T$ , relative changes in temperature needs ;  $\Delta EIV_N$ , relative changes in nitrogen needs.

	$\Delta EIV_L$	$\Delta EIV_T$	$\Delta EIV_N$
<i>Selected predictors</i>	<i>No fixed effects selected</i>	<i>No fixed effects selected</i>	<i>No fixed effects selected</i>
Observations	108	108	108
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.000 / 0.31	0 / 0.34	0 / 0.44

Table S5 Selected fixed effects of the Community Weighted Mean relative differences in the 1980s and the 2020s.  $\Delta EIV\_F$ , relative changes in soil moisture needs.

	<b><math>\Delta EIV\_F</math></b>	<b><math>\Delta</math>Flowering onset</b>	<b><math>\Delta</math>Flowering duration</b>
<i>Selected predictors</i>	<i>No fixed effects selected</i>	<i>No fixed effects selected</i>	<i>No fixed effects selected</i>
Observations	108	108	108
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0 / 0.31	0 / 0.34	0 / 0.29

## **Partie 2 – Influence des communautés adventices des vignobles sur les processus de recyclage de la matière organique**



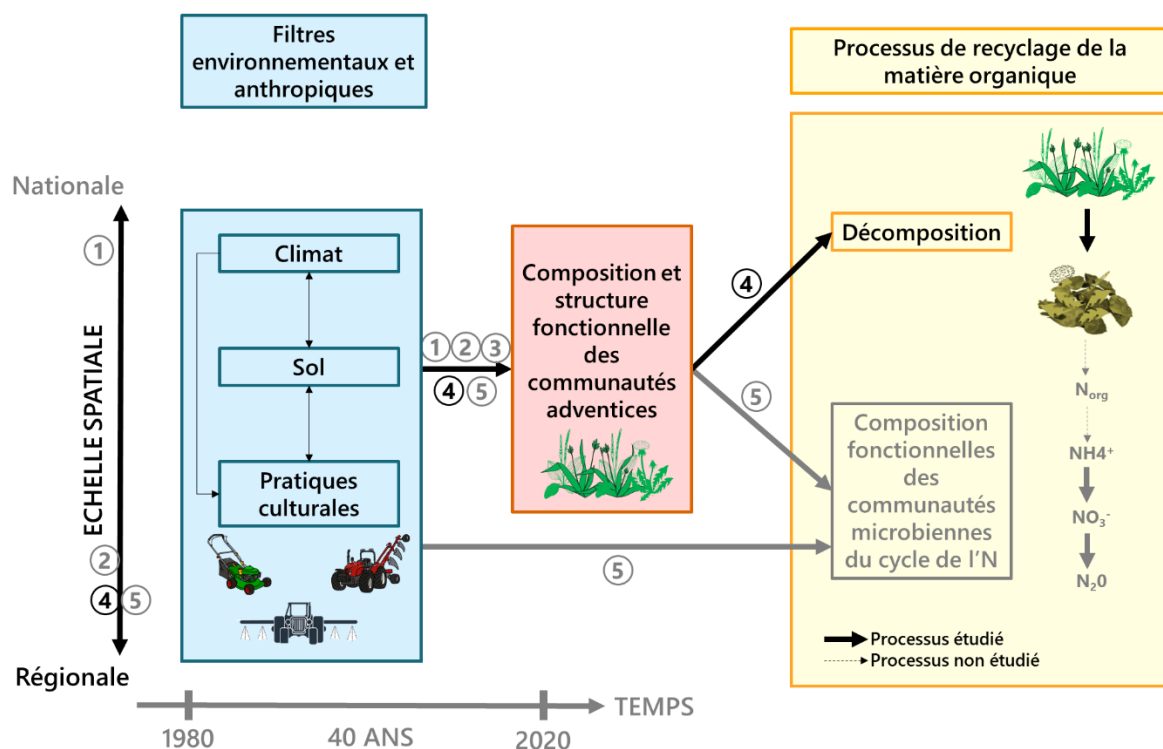
Une des communautés adventices d'une parcelle viticole enherbée dans le Montpelliérais

Photo de Guillaume Fried (mars 2020)



# Chapitre 4 – Linkages between traits and decomposition of weed communities along a soil management and pedoclimate gradient in Mediterranean vineyards

Bopp, M.-C., Fried, G., Metay, A., Bastianelli, D., Bonnal, L., & Kazakou, E. (2022). Linkages between traits and decomposition of weed communities along a soil management and pedoclimate gradient in Mediterranean vineyards. *Annals of Botany*. <https://doi.org/10.1093/aob/mcac099>







## **Présentation du chapitre**

Ce chapitre est basé sur un jeu de données de relevés floristiques (n=51 communautés) de la région du Montpelliérais (16 parcelles de vignes), observés en mars 2020. Une série de traits a été mesurée dans les parcelles de vignes. **L'objectif de cette étude est de comprendre les effets indirects des pratiques de gestion, de fertilisation et des conditions pédoclimatiques sur la décomposabilité des communautés adventices via leurs propriétés fonctionnelles aériennes.**

**Les hypothèses de cette étude sont:**

- (i) Les communautés adventices localisées dans les vignes travaillées et désherbées chimiquement développent des stratégies acquisitives et sont plus décomposables,
- (ii) Les communautés adventices localisées dans les vignes tondues développent des stratégies conservatives et sont moins décomposables.

Nous démontrons que le travail du sol et la tonte filtrent des communautés adventices plus décomposables par rapport aux communautés issues de parcelles viticoles désherbées chimiquement (16% et 8% de perte de masse supérieure après deux mois de décomposition, respectivement) (Figure 21). L'analyse de piste sélectionne le type de pratique de gestion des adventices comme le facteur principal déterminant la perte de masse *via* son effet sur les propriétés fonctionnelles, tandis que le pédoclimat a des effets mineurs. Le désherbage chimique favorise les communautés ayant un investissement plus élevé dans les feuilles résistantes (par exemple, 38% de lignine:N en plus, 22% de teneur en azote foliaire en moins), ce qui entraîne une perte de masse plus faible par rapport aux communautés issues de parcelles viticoles travaillées et tondues. Si les pratiques affectent significativement la diversité fonctionnelle foliaire des communautés adventices, cette dernière n'est pas significativement reliée à la décomposition potentielle.

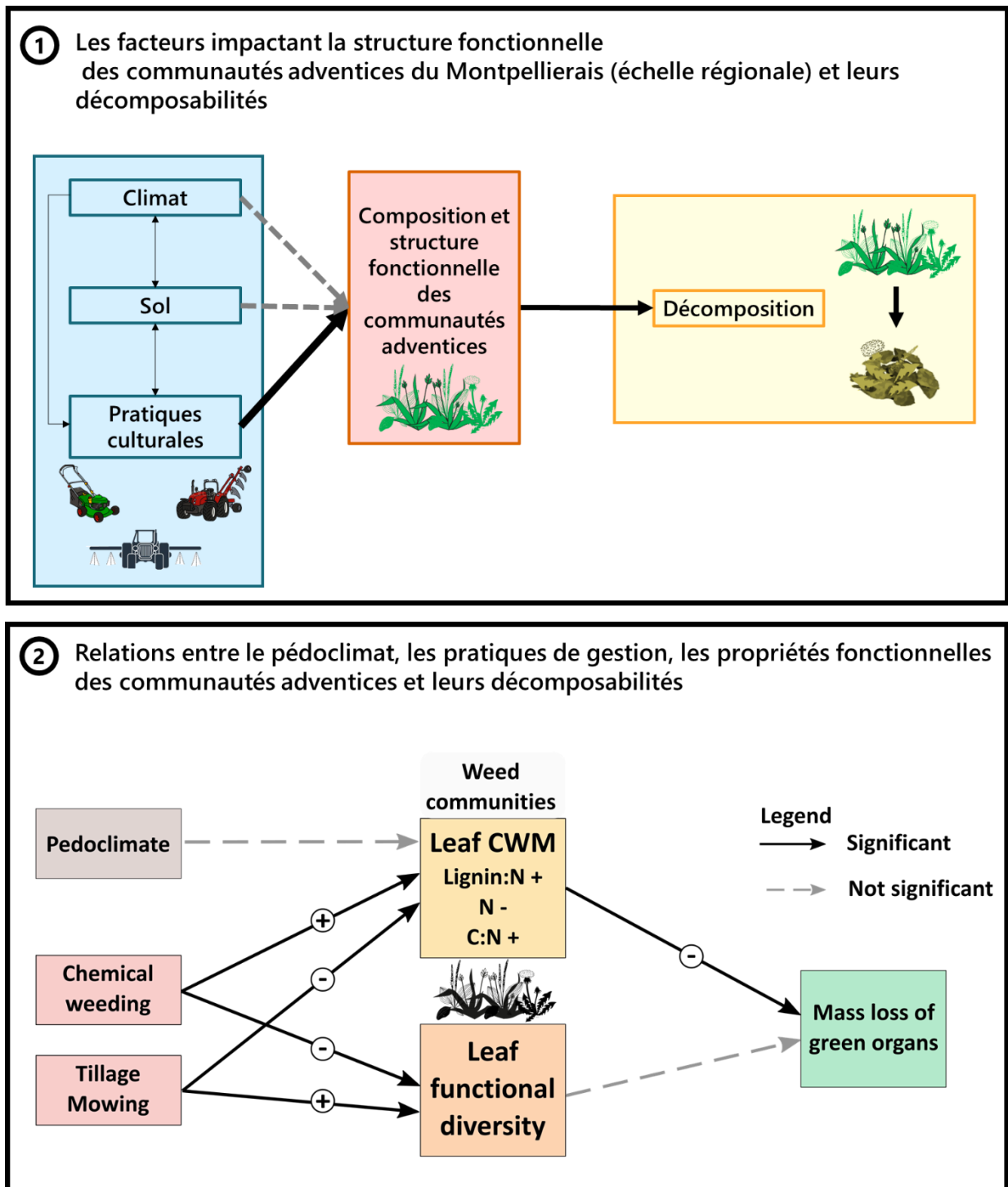


Figure 21 Résumé graphique du chapitre 4. (1) Les pratiques de gestion des adventices sont le facteur principal déterminant la perte de masse via son effet sur les propriétés fonctionnelles, tandis que le pédoclimat a des effets mineurs. (2) La décomposabilité (« mass loss of green organs ») est associée aux moyennes pondérées à l'échelle de la communauté des ratios lignine foliaire et azote foliaire (Lignin:N), la teneur en azote (N) et le ratio carbone et azote foliaire (C:N). Les communautés adventices issues de parcelles viticoles désherbées ont des Lignine:N, C:N élevés et de faibles N et sont faiblement décomposables. Au contraire, les communautés issues de parcelles viticoles travaillées et tondues ont de faibles Lignine:N, C:N et des N élevés et sont fortement décomposables. Si les pratiques impactent significativement la diversité fonctionnelle foliaire des communautés adventices, cette dernière n'est pas significativement reliée à la décomposabilité.

## Linkages between traits and decomposition of weed communities along a soil management and pedoclimate gradient in Mediterranean vineyards

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- **Background and Aims** Decomposition is a major ecosystem process which improves soil quality. Despite that, only a few studies have analysed decomposition in an agricultural context, while most agrosystems (e.g. vineyards) are facing decreasing soil quality. The objective of this study is to understand the impacts of both pedoclimate and weed management on the mass loss of vineyard weed communities during the early stages of the decomposition process through their functional properties.
- **Methods** In 16 Mediterranean vineyards representing both a pedoclimate and a soil management gradient, we measured the mass loss of green above-ground biomass of 50 weed communities during decomposition in standard conditions and key leaf traits of dominant species [e.g. leaf dry matter content (LDMC) and leaf lignin to nitrogen ratio (lignin:N)]. Both the mean [i.e. community-weighted mean (CWM)] and diversity (i.e. Rao index) were computed at the community level. Path analysis was used to quantify the effects of agro-environmental filters on the mass loss of weed communities through their functional properties.
- **Key Results** Tillage and mowing filtered more decomposable communities than chemical weeding (16 and 8 % of higher mass loss after 2 months of decomposition). Path analysis selected weed management practice type as the main factor determining mass loss through its effect on functional properties, while soil and climate had minor and no effects, respectively. Chemical weeding favoured communities with higher investment in resistant leaves (e.g. 38 % higher lignin:N, 22 % lower leaf nitrogen content) which resulted in lower mass loss compared with tilled and mowed communities. Mowing favoured communities with 47 % higher biomass and with 46 % higher nitrogen content.
- **Conclusions** Weed management significantly influenced weed mass loss, while the pedoclimate had little effect. Our results suggest that mowing is a promising alternative to herbicide use, favouring higher biomass, nitrogen content and decomposability potential of weeds.

**Key words:** Mass loss, decomposition, weeds, vineyards, trait-based approach, community-weighted means, Rao, functional diversity, soil management practices, soil characteristics, climate.

### INTRODUCTION

Understanding how weed communities respond to environmental filtering in agrosystems (e.g. annual crops or perennial crops) and affect ecosystem processes is essential to designing and managing agroecosystems (Damour *et al.*, 2018). In these systems, both environmental conditions (e.g. climate and soil characteristics) and agricultural practices (e.g. weed management) filter weed species according to their trait values, resulting in constrained functional properties at the community level (Booth and Swanton, 2002). Mediterranean vineyard flora is a relevant model to better understand both weed response to these agro-environmental filters and weed effects on the processes occurring in agrosystems. Indeed, the Mediterranean climate exerts strong environmental filters on the plant communities such as summer drought filtering (de la Riva *et al.*, 2016) to which species must adapt through their

trait values (Rota *et al.*, 2017). Moreover, weed management is quite diversified in vineyards (Winter *et al.*, 2018): recent studies showed that each weed management type (i.e. chemical weeding, tillage and mowing) filters weed functional properties in different ways (MacLaren *et al.*, 2019; Hall *et al.*, 2020; Guerra *et al.*, 2021; Bopp *et al.*, 2022). For instance, tillage exerts strong and frequent disturbance on weed communities (Gaba *et al.*, 2014; Kazakou *et al.*, 2016). Such a highly disturbed environment favours acquisitive species with high photosynthetic activity per unit of dry mass invested in the leaves [high specific leaf area, i.e. leaf area to leaf dry mass; and low leaf dry matter content (LDMC), i.e. leaf dry mass to leaf fresh mass ratio] (Kazakou *et al.*, 2016; Hall *et al.*, 2020; Guerra *et al.*, 2021; Bopp *et al.*, 2022). On the contrary, mowing removes partially weed biomass and can be considered a disturbance with lower intensity compared with tillage (Kazakou *et al.*, 2016). Several studies demonstrated

that weed communities developing in mowed vineyards had more conservative strategies, producing more expensive and resistant leaves, that are consequently less efficient for the photosynthesis per unit of dry mass (high LDMC and low specific leaf area) (Kazakou *et al.*, 2016; Hall *et al.*, 2020; Mainardis *et al.*, 2020; Guerra *et al.*, 2021; Bopp *et al.*, 2022). The strategies that weed communities can develop under chemical weeding are less clear. Even if herbicides can also be considered as high-intensity disturbances as the whole weed biomass is destroyed (Gaba *et al.*, 2014), studies found contrasting results: more acquisitive strategies (Hall *et al.*, 2020; Bopp *et al.*, 2022) or more conservative strategies (MacLaren *et al.*, 2019; Guerra *et al.*, 2021).

Vineyards are facing major soil quality issues due to management intensification, and studying how weed management could improve soil quality is of utmost importance (Garcia *et al.*, 2018; Novara *et al.*, 2018). In vineyards, weed biomass is destroyed by management practices before plant senescence. The biomass is returned to the soil and can therefore be used as green manure to improve soil quality (Steenwerth *et al.*, 2016). Weed decomposition is one of the major processes involved in nutrient and carbon cycling (Buchholz *et al.*, 2017; Pingel *et al.*, 2019) and to a certain extent soil organic matter (SOM) and nutrient availability (Liu *et al.*, 2020). In Californian vineyards, Steenwerth *et al.* (2016) demonstrated that the above-ground biomass of the weeds contained 93 kg ha<sup>-1</sup> of nitrogen, which could contribute to meeting the nitrogen requirement of the vineyards (20–90 kg N ha<sup>-1</sup>) (Metay *et al.*, 2014; Verdenal *et al.*, 2021). However, to our knowledge, no study has assessed the decomposition potential of the biomass produced by weeds in vineyards.

In natural and semi-natural ecosystems, the links between traits and decomposition have been largely studied on litters, naturally occurring in these extensively managed systems. Historically, litter decomposition has been mostly explained by litter traits (e.g. Melillo *et al.*, 1982; Gallardo and Merino, 1993), but several studies have shown that green leaf traits related to plant resource-use strategies were also good predictors (e.g. Cornelissen and Thompson, 1997; Kazakou *et al.*, 2006). Leaf structural traits such as LDMC quantify plant investment in tough, resistant and long-lived leaf structures leading to low decomposition potential (Garnier *et al.*, 2004; Kazakou *et al.*, 2006, 2009). These structural leaf traits

were also found to relate to leaf fibre content (lignin, hemicellulose and cellulose) which was also negatively correlated with decomposition (Kazakou *et al.*, 2006; Kurokawa and Nakashizuka, 2008; Bumb *et al.*, 2018). Other chemical traits such as leaf nitrogen content (LNC) are also good predictors of decomposition (Freschet *et al.*, 2010). Indeed, LNC is related to nutrient acquisitive strategies associated with low leaf carbon investment in leaf structure leading to high decomposition potential (Cornwell *et al.*, 2008; Eichenberg *et al.*, 2015).

To scale up from species to community scale, the mass ratio hypothesis states that trait values of the most dominant species within the communities are the main drivers of ecosystem processes (Grime, 1998; Garnier *et al.*, 2004). Thus, it is expected that the community-weighted means (CWM, i.e. species-specific mean leaf trait values weighted by the abundance in the community) of traits related to decomposition would drive the decomposition process (Garnier *et al.*, 2004; Fortunel *et al.*, 2009). In addition to considering the trait values of the dominant species of communities, the variability of trait values within communities might give a complementary understanding of the mechanisms driving decomposition (García-Palacios *et al.*, 2017). Indeed, a recent meta-analysis demonstrated that mixed litters (i.e. composed of several species) decomposed from 2 % to 4 % more rapidly than the expected average value of decomposition from single-species litter experiments (Liu *et al.*, 2020). This synergistic effect of litter mixing can be explained by higher trait dissimilarities (Porre *et al.*, 2020). Rao's quadratic entropy (Rao), i.e. the average of trait dissimilarity represented by the different species making up a community (Botta-Dukát, 2005), is an index widely used to measure the dissimilarity of single-trait or multi-trait value distributions (de Bello *et al.*, 2016). For instance, LNC variability was found to be positively correlated with decomposition (Plazas-Jiménez and Cianciaruso, 2021). This synergistic effect was explained by nutrient transfers from high-quality litters (high LNC, low leaf lignin:N) to low-quality litters under nutrient-limited conditions, resulting in an overall higher decomposition (Handa *et al.*, 2014; Finerty *et al.*, 2016). In contrast, the release of inhibitory secondary compounds (e.g. lignin and polyphenols) may induce antagonist effects (Hättenschwiler *et al.*, 2005; Kou *et al.*, 2020).

The general objective of the present study was to understand the indirect impacts of weed management, fertilization

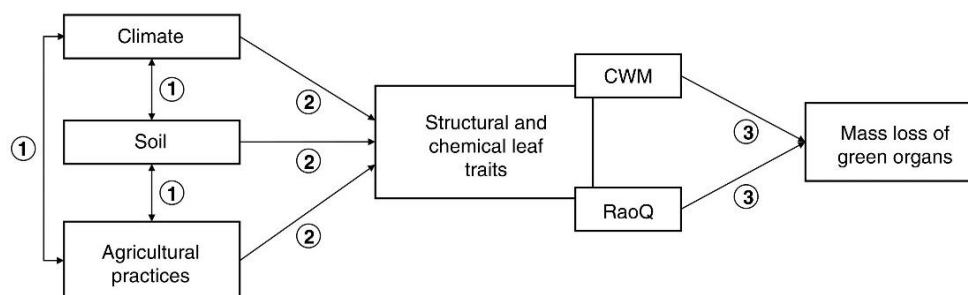


FIG. 1. Relationships between climate, soil, and agricultural practice drivers, structural and chemical leaf traits and the mass loss of green organs of weed communities in vineyards. In this conceptual framework, we assume that the mass loss of green organs is impacted by agro-environmental filters through their effect on the functional properties of plant communities (arrows 2) and the relationships between the functional properties and the mass loss of green organs (arrows 3). We also assume that agro-environmental drivers (arrows 1) interact with each other. CWM, community-weighted mean; RaoQ, Rao quadratic entropy.

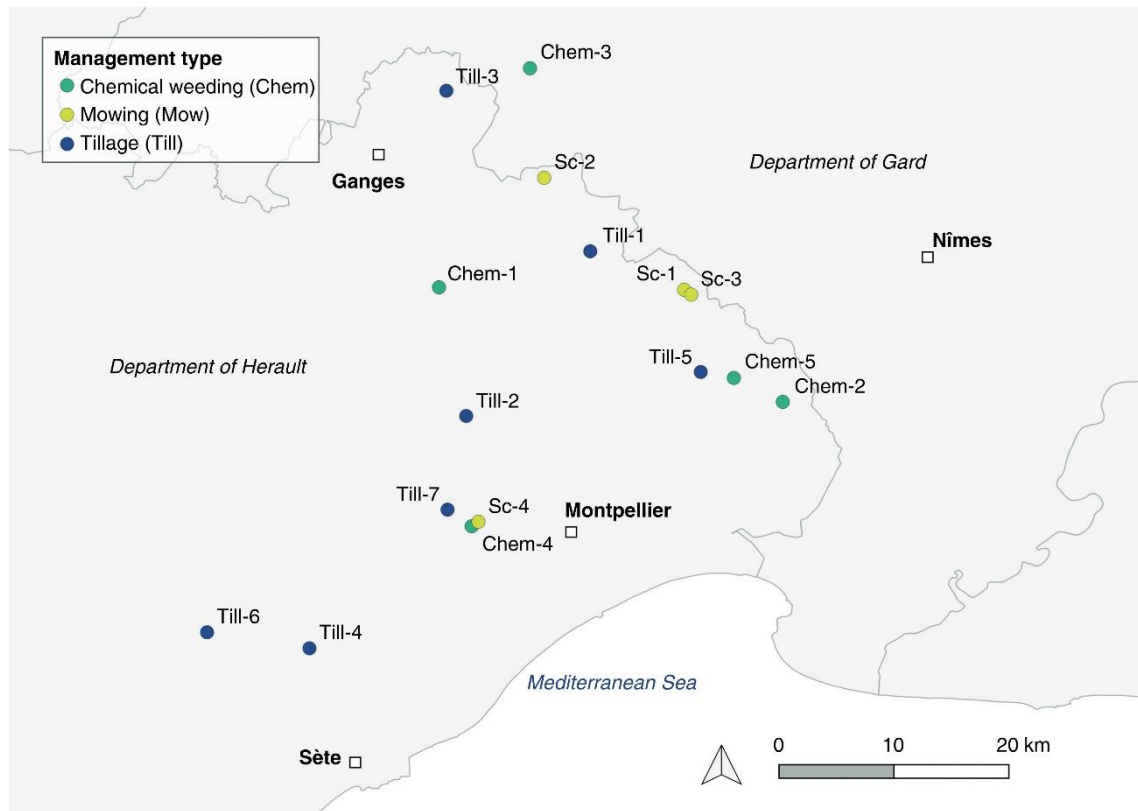


FIG. 2. Location of the 16 vineyards near Montpellier, France. The dark blue dots are the seven vineyards (Till-1, Till-2, Till-3, Till-4, Till-5, Till-6 and Till-7) where tillage is the prevailing weed management practice of inter-rows. The light blue dots are the five vineyards (Chem-1, Chem-2, Chem-3, Chem-4 and Chem-5) where chemical weeding is applied once a year. The green dots are the four vineyards (Mow-1, Mow-2, Mow-3 and Mow-4) with permanent spontaneous cover managed by mowing.

and pedoclimatic conditions on mass loss of ‘green’ weed biomass through several leaf functional properties (CWM and Rao) (Fig. 1). In tilled and chemically weeded vineyards (i.e. disturbed environments), we expected that communities would develop acquisitive strategies with a high photosynthesis rate per unit of invested dry mass [high LNC, low LDMC, low leaf fibre content and low leaf carbon to nitrogen ratio (C:N)] and thus high decomposability. In contrast, we hypothesized that mowing would select communities composed of species with conservative strategies, with lower photosynthetic activity per unit of dry mass and more resistant leaves (higher LDMC, higher fibre content, lower LNC and higher leaf C:N), resulting in a lower mass loss potential through decomposition. To test these hypotheses, we assessed the mass loss of 50 communities after 2 months of decomposition, with biomass that was sampled before the senescence in a network of 16 Mediterranean vineyards characterized by a pedoclimate and weed management gradient. We first assessed how agricultural practices (weed management) and pedoclimate affected the weed community functional properties (Fig. 1, arrows 2), considering possible interactions between agro-environmental filters (Fig. 1, arrows 1). We then explored the relationships between weed community functional properties and weed mass loss

through decomposition (Fig. 1, arrows 3). Finally, we tested the overall framework using path analysis.

## MATERIALS AND METHODS

### *Pedoclimate characterization of the vineyard network*

Plant material was collected in 16 vineyards around Montpellier, France (Fig. 2). The Mediterranean climate of this region is warm (mean annual temperature of 14.7 °C) and quite dry (annual rainfall of 818 mm with 33 % of the rainfall occurring in October and November) with a mean aridity index of 0.68 (i.e. the ratio between annual rainfall and potential evapotranspiration) (Table 1). The soil was sampled from the 0–10 cm topsoil layer within the inter-rows of the vineyards (i.e. the free space between the rows of the vines): ten samples were collected in different inter-rows within the same vineyard and mixed to get one sample per vineyard. Thus, in total, measurements were conducted on 16 soils. Soil textures (NF X 31-107 method), SOM (NF ISO 14235) and pH (NF ISO 10390) of the 16 samples were measured. The vineyard network is characterized by a wide range of soil textures, from sandy soils near the Mediterranean Sea to clayey and silty soils on the northern part

of the network (Table 1). The organic matter content of soils is quite low ( $19.2 \text{ g kg}^{-1}$  on average) but is highly variable among the vineyards (from  $7.6$  to  $50 \text{ g kg}^{-1}$ ). Soils are mostly alkaline (pH mean value of 8.3).

#### Weed management and fertilization practices within the vineyard network

Weed management and fertilization practices were recorded through surveys of the 16 farmers of the network. The questionnaire was composed of 61 questions with open and multiple-choice answers divided into three sections: (1) farm characteristics (area, wine valorization and labels); (2) vineyard characteristics (topography, vine density, grape variety, fertilization, manure and irrigation); and (3) cultural calendar of weed management practices of rows and inter-rows from 2015 to 2020 (type and date of each practice, agricultural machinery, the dose of chemical weeding, the type of herbicide used and the depth of tillage).

In this study, we selected two types of soil management practice variables in the inter-rows: (1) four variables that characterize the disturbance gradient of the vineyard network described by weed management practice types (tillage, chemical weeding and mowing) and weed management frequency; and (2) one variable quantifying fertilization related to the gradient of the management of soil nutrient resources by farmers (Table

2). The frequency of weed management disturbance was assessed using the annual number of weed management practices in the inter-rows: the number of chemical weeding (Nb.Chem), tillage (Nb.Till) and mowing (Nb.Mow). Moreover, the annual longest period between two weed destructions by tillage or chemical weeding (Sc.dur) was used to describe the overall inverse of frequency-disturbing events at the inter-row level. Mowing was not considered a totally destructive disturbance because it partially removes weed biomass. Fertilization was described by the annual nitrogen fertilization input (Ferti). To consider the cropping system history of each vineyard, each soil management variable was quantified and averaged over the last 5 years before the sampling. A principal component analysis (PCA) was performed based on all these scaled variables (PCA function of the FactoMineR R package) and hierarchical clustering was carried out on the first two axes of the PCA to define groups of vineyards sharing similar agricultural practices (HCPC function of the FactoMineR R package) (Le et al., 2008). Three main management types were selected by the hierarchical clustering (Supplementary Data Fig. S1). Cluster 1 groups seven vineyards dominated by tillage practice and higher nitrogen input than the other vineyards over the 5 last years before the experiment (Till-1, Till-2, Till-3, Till-4, Till-5, Till-6 and Till-7), cluster 2 includes four vineyards managed by mowing (Sc-1, Sc-2, Sc-3 and Sc-4) and cluster 3 gathers the five chemically weeded vineyards (Chem-1, Chem-2, Chem-3, Chem-4 and Chem-5) (Fig. 2).

TABLE 1. Range of climate and soil characteristics of the 16 vineyards

Factor type	Variables	Abbreviation	Unit	Mean (min–max)	Coefficient of variation
Climate	Mean annual temperature	–	°C	14.7 (13.7–15.9)	5.0 %
	Annual rainfall	–	mm	818 (554–929)	14.3 %
	Aridity index	AI	–	0.68 (0.45–0.82)	18.0 %
Soil	Silt content	Silt	$\text{g kg}^{-1}$	356 (146–634)	30.7 %
	Sand content	Sand	$\text{g kg}^{-1}$	429 (174–704)	30.6 %
	pH	pH	–	8.3 (6.7–8.8)	6.7 %
	Soil organic matter	SOM	$\text{g kg}^{-1}$	19.2 (7.6–50.0)	48.7 %

The climatic data were extracted from the SAFRAN grid of Météo France from 2015 to 2020 (Quintana-Seguí et al. 2008).

TABLE 2. Characteristics of weed management and fertilization practices within the vineyard network (mean, minimum and maximum) per weed management type

Management variables	Chemical weeding (Chem) mean (min–max)	Mowing (Mow) mean (min–max)	Tillage (Till) mean (min–max)
Annual number of tillage of inter-rows (Nb.Till)	0.1 (0–0.5)	0	2.5 (1.2–4.3)
Annual number of mowing of inter-rows (Nb.Mow)	0.7 (0–1.5)	2.2 (1–4)	0.7 (0–1.5)
Annual number of chemical weeding of inter-rows (Nb.Chem)	1.0 (0.8–1)	0	0.16 (0–0.5)
Number of days of the most extended period between two weed destructions by tillage or chemical weeding (Sc.dur)	308 (195–341)	365	189 (127–269)
Annual nitrogen fertilization input in $\text{kg ha}^{-1}$ (Ferti)	6.9 (0–14.6)	3.2 (0–12.9)	9.2 (0.7–18.2)

All the variables were averaged over the period 2015–2020.

### Characterization of covariations of the soil, climate and weed management practices

Covariations between soil management (number of tillage operations, mowing, chemical weeding and fertilization input), soil characteristics (soil organic matter, pH, sand and silt percentage of soils) and climate (aridity index) were investigated by performing a PCA including all these variables (see [Supplementary data Fig. S2](#) for more details) and the significance of the correlations was estimated using the Pearson correlation test with *P*-values corrected using the Holm method ([Supplementary data Table S1](#)). Only three correlations were significant: a negative correlation between silty and sandy soils (correlation coefficient:  $-0.77$ ); a negative correlation between sandy soils and mowing (correlation coefficient:  $-0.75$ ); and a negative correlation between tillage and the maximum duration of spontaneous cover cropping (correlation coefficient:  $-0.89$ ).

### Floristic composition of weed communities

In each vineyard, four quadrats of  $60 \times 60$  cm were randomly placed in neighbouring inter-rows, delimiting four distinct weed communities per vineyard. In total, 64 weed communities (4 quadrats  $\times$  16 vineyards) were characterized in the vineyard network and 82 species were identified. We sampled plant communities in March 2020 before the first weed management practices. In each quadrat, the plant species were identified and their covers were quantified to estimate their relative abundances. Applying the mass ratio hypothesis ([Grime, 1998](#)), we identified the list of the most abundant species for each community that covered at least 80 % of the quadrats to measure their leaf traits ([Garnier et al., 2004](#)). As there were missing data, to reach 80 % of the communities with trait values, we only kept the quadrats for which we had the trait values to reach 80 % of the cover for the result analyses (in total 50 quadrats of the 64).

### Measurement of mass loss of green organs during decomposition

To assess decomposition potential, we set up a standardized laboratory bioassay following [Wardle et al. \(1998\)](#) by controlling temperature and humidity, with similar soil conditions and decomposer populations, while maintaining a sufficiently natural situation so that the results of bioassay tests may be extrapolated to the field situation. This bioassay has the advantage of measuring mass loss as influenced by biomass quality in a shorter period than in 'litter beds' [8 weeks of incubation in microcosms corresponds to 9 months of incubation in 'litter beds' in the Mediterranean climate ([Kazakou, 2006](#)), data not shown]. To quantify the potential decomposition of the 'fresh' or 'green' biomass that would constitute the mulch after mowing, the above-ground parts of all the weeds of the community (leaves, stems and reproductive parts) were collected and dried at  $60^\circ\text{C}$ . We dried the sampled biomass to homogenize the humidity of the biomass (some samples were collected during rainy days) and to prevent the decomposition to start for biomass that was sampled earlier in the season than others (2 weeks of sampling in total). From 1.5 to 2 g of this dry 'green' biomass which mixed leaves, stems and reproductive parts of

the communities (4 replicates  $\times$  50 communities = 200 samples) were placed inside thin litter nylon bags of 0.3 mm mesh and  $5 \times 5$  cm<sup>2</sup> (Northern Mesh, Oldham, UK) on 9 cm diameter Petri dishes, filled with the same standardized humus substrate (3:1 mixture of mineral soil and surface organic horizon) following the methodology of [Wardle et al. \(2002\)](#). The effect of macro- and mesofauna was excluded by the small holes in the litter bags (0.3 mm) and the conditions of the experiment (Petri dishes in closed climate chambers). Each 'dry green' biomass put in the litter bags was weighed before the beginning of the experiment ( $M_i$ ). The Petri dishes were then sealed and kept in the dark at  $24^\circ\text{C}$  for 2 months. The soil moisture was kept constant with weekly watering (200 % of field capacity). Thus, in these optimal and constant conditions, the differences in the potential mass loss were mainly due to the differences in the quality of the decomposing green material. At the end of the experiment, we weighed the green mass ( $M_f$ ) after decomposition. We defined the metric of decomposition potential as 'mass loss of green organs' because the measurements were done on the green above-ground biomass, mixing all organs, before their senescence. The percentage of mass loss of green organs (MLGO) was calculated as:

$$\text{MLGO} = 100 \times [1 - (M_f - M_i) / M_i] \quad (1)$$

where  $M_i$  is the 'dry green' mass before decomposition sampled in the quadrats (g) and  $M_f$  is the 'dry green' mass after 2 months of decomposition (g).

### Functional properties of weed communities

Four leaf traits were measured on the 51 dominant species representing 80 % of the relative cover within each of the 50 communities (see the detailed list of the sampled species in [Supplementary data Table S2](#)). The LDMC represents the proportion of light and cheap tissues (mesophyll and epidermis) with regard to dense and costly tissues (vascular tissues and sclerenchyma) ([Kazakou et al., 2006](#)). Leaf cellulose content (Cel), leaf hemicellulose content (Hemicel) and leaf lignin content (Lignin) were also measured to assess the leaf composition of fibres, from easily degradable fibres (i.e. cellulose) to more recalcitrant fibres (i.e. lignin). Leaf carbon content, LNC and leaf C:N were also selected. The C:N describes the investment in carbon in the leaf structure (conservative strategy) with regards to the leaf investment in photosynthetic enzymes (acquisitive strategy). The leaf lignin:N was also computed, as this trait indicates the leaf carbon quality rather than its quantity as in the C:N ([Chapin et al., 2012](#)). Indeed, the complex and variable structure of lignin makes it the most difficult leaf fibre to decompose ([Krishna and Mohan, 2017](#)).

The LDMC was measured on the leaves of eight individuals per species collected in the inter-rows of the vineyards (i.e. the free space between the rows of the vines) where the species were dominant, following [Pérez-Harguindeguy et al., 2013](#)). Thus, for the most frequent dominant species of the vineyard network, this trait was measured in several vineyards (for instance, eight individuals of *Crepis sancta* were collected in six different vineyards; thus 48 individuals were measured for this species). The LNC and the leaf carbon content were measured pooling all the eight individual leaves per



species (or more if the species was measured in several vineyards) with three repeated measures by elemental analysis (NF ISO 10694) using a FrashEA® 112 analyser. The leaf cellulose, hemicellulose and lignin content were also measured at the species level on the pooled samples of leaves. These traits were analysed using near-infrared reflectance spectroscopy (NIRS) following [Bumb et al. \(2016\)](#). Dried and ground samples of each species were placed in quartz ring cells and spectra were collected with a FOSS Nirsystem 6500 spectrometer (FOSS Nirsystems, Silver Spring, MD, USA) operating from 400 to 2500 nm in reflectance mode. Leaf cellulose and lignin contents were determined with the use of existing calibrations at CIRAD (French International Centre of Agricultural Research for Development, Montpellier, France). Moreover, the nitrogen content of the above-ground biomass collected in the quadrats was also assessed to quantify the potential green manure effect of the weeds in vineyards using the same method as for the leaves. To calculate the nitrogen content of the above-ground biomass in more classical agronomic units, we extrapolated the nitrogen content of this biomass sampled in 60 × 60 cm<sup>2</sup> quadrats in kilograms per hectare.

To assess litter quality at the community level, we calculated the CWM of the leaf traits ([Garnier et al., 2004](#)) applying the mass ratio hypothesis which states that the most dominant species of a community drive the ecosystem processes ([Grime, 1998](#)):

$$\text{CWM} = \sum_{i=1}^n p_i \times \text{trait}_i \quad (2)$$

where  $p_i$  is the relative abundance of the species  $i$  within a community,  $\text{trait}_i$  is the value of trait of the species  $i$  and  $n$  is the number of species within the community. The CWM expresses the most probable trait value of an individual plant within a community ([Garnier et al., 2004](#)). To consider the effect of functional diversity on decomposition, we computed Rao's quadratic entropy (Rao's Q) ([Botta-Dukát, 2005](#)) for each leaf trait using the dbFD function from the FD R package ([Laliberté and Legendre, 2010](#); [Laliberté et al., 2014](#)).

$$\text{Rao} = \sum_{i=1}^n \sum_{j=1}^n p_i p_j d_{ij} \quad (3)$$

where  $n$  is the number of species in a community,  $d_{ij}$  the dissimilarity between each pair of different species  $i$  and  $j$ , and  $p_i$  and  $p_j$  are the relative cover of species  $i$  and  $j$ , respectively, within the communities. The descriptive statistics of each CWM and Rao are presented per weed management type in [Supplementary data Table S3](#) at the community level.

To characterize the functional space of the CWM and Rao index following [Migliorini and Romero \(2020\)](#) and [García-Palacios et al. \(2017\)](#), we computed a PCA based on each CWM and Rao indices, considering covariations between CWM and Rao indices for each trait. In the CWM functional space, we selected the first two axes that explained most of the functional variance (79.3 %) ([Fig. 3](#)). The first axis (CWM1) was mostly determined by the weighted means of lignin:N, C:N and LNC. The second axis (CWM2) was driven by the weighted means of hemicellulose content and LDMC. In the Rao functional space,

the functional diversity of each trait was mostly driven by the first two axes (68.4 %) ([Fig. 3](#)). The first axis (Rao1) was determined by the Rao of lignin:N, C:N and LNC. The second axis (Rao2) was mostly driven by the Rao of the leaf hemicellulose and the lignin content.

#### Data analyses

To quantify the relationships between (1) the mass loss of green organs and the functional properties (coordinates of communities along the PCA axes based on CWM and Rao indices) and (2) agro-environmental filters and functional properties, linear mixed models were used employing the lme function from the lme4 R package ([Bates et al., 2015](#)). A 'vineyard' random effect was added before model selection to consider the hierarchical structure of our dataset (four quadrats maximum per vineyard). Before model construction, the collinearity of explanatory variables was investigated using the variance inflation factor (VIF < 5). Model selection was performed using a backward step selection procedure based on the corrected Akaike information criterion (AICc). To compare the effects of weed management on the mass loss, the biomass and its nitrogen content, we also used linear mixed models with 'vineyard' as a random effect. Analysis of variance (ANOVA) was used to detect the significance of the effect of weed management, and a pairwise Student  $t$ -test was performed to compare the average mass loss, biomass and its nitrogen content according to the different weed management types.

A path analysis was performed to quantify the influence of agro-environmental filters on the mass loss of green organs through changing the functional properties of communities using the psem function from the piecewiseSEM R package ([Lefcheck, 2016](#)). This function uses a path analysis method that allows dealing with the hierarchical structure of the dataset. It applies the directed separation method proposed by [Shipley \(2009\)](#) which tests that all variables are conditionally independent. To do this, a set of conditional independence claims called the 'basis set' is identified from the hypothesized path diagram. A Fisher's  $C$  statistic is then calculated using all the  $P$ -values of the tests of each independent claim constituting the 'basis set'. The  $C$  statistic is compared with  $\chi^2$  distribution with  $2k$  degrees of freedom ( $k$  is the number of independent claims). The path diagram is considered significant if the probability that the relationships within the independent claims occur, is weak ( $P$ -value > 0.05). Before model selection, we added a 'vineyard' random effect in each sub-model constituting the path analysis to consider the hierarchical structure of our dataset. We also added correlated errors between CWM1 (coordinates on the first axis of the CWM PCA), CWM2 (coordinates on the second axis of the CWM PCA), Rao1 (coordinates on the first axis of the Rao PCA) and Rao2 (coordinates on the second axis of the Rao PCA) and between each agro-environmental filter to consider non causal covariations. In the initial hypothesized structural equation model, we only added the functional properties which were found to be significantly related to the mass loss of green organs based on the linear mixed models. All data analyses were carried out using R version 4.1.1 ([R Core Team, 2021](#)).

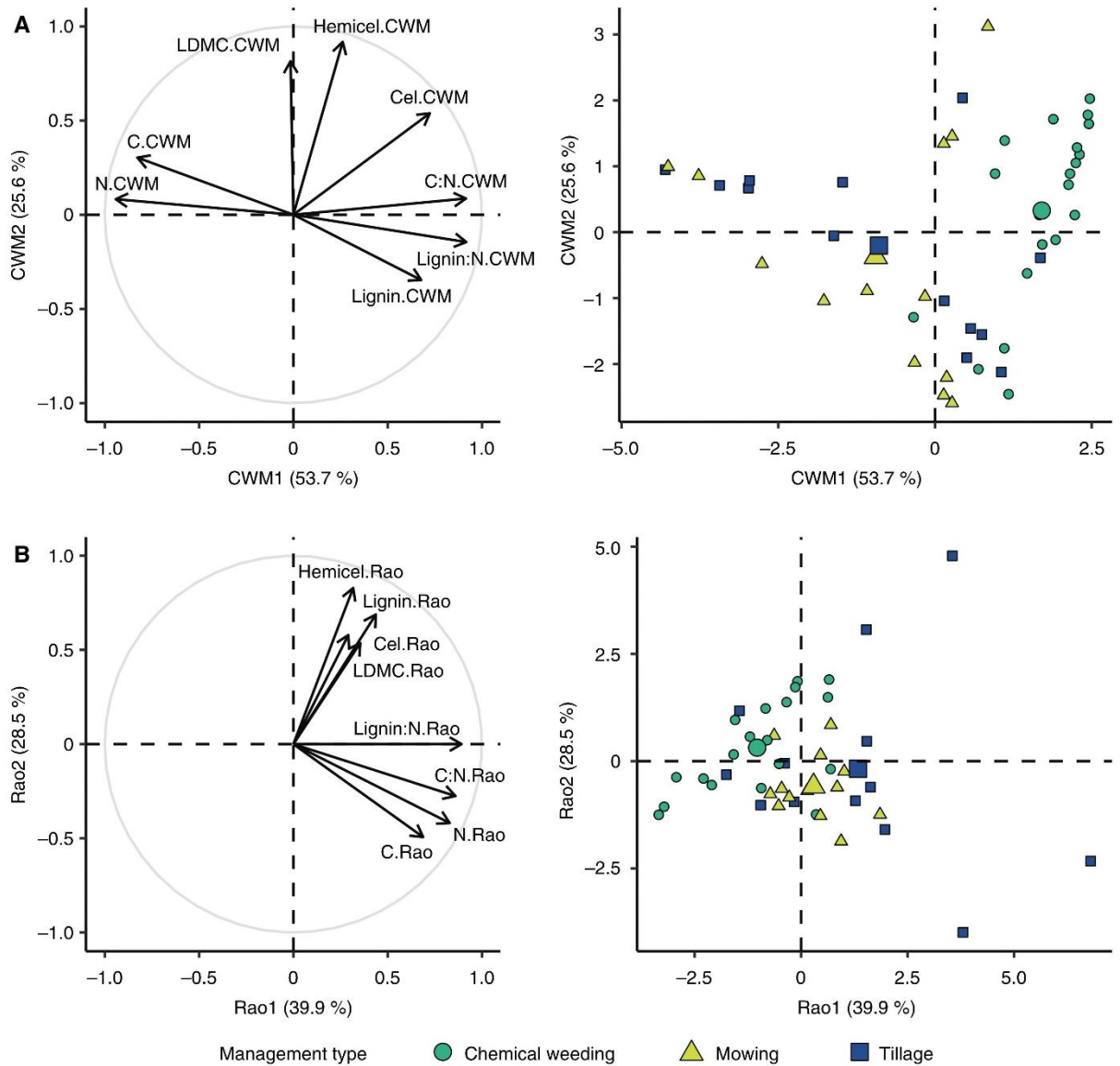


FIG. 3. (A) PCA based on community-weighted means (CWM). Weed communities are displayed in the CWM functional space ( $n = 50$ ). (B) PCA based on Rao indices for each trait. Weed communities are displayed in the Rao functional space ( $n = 50$ ). The colours of each dot refer to the management type of the vineyard where the community was located. The large symbols are the barycentres of the communities from the three groups of management. LDMC, leaf dry matter content; C, leaf carbon content; N, leaf nitrogen content; Lignin, leaf lignin content; lignin:N, leaf lignin to nitrogen ratio; C:N, leaf carbon to nitrogen ratio; Cel, leaf cellulose content; Hemicel, leaf hemicellulose content.

## RESULTS

### *Mass loss of green organs varied with the vegetation management practices*

The mass loss of green organs of the weeds varied from 33 % of decomposed biomass to 60 %, with an average of 45 %, after 2 months of decomposition in optimal conditions. The mass loss of green organs was significantly impacted by weed management types (Supplementary data Table S4). Communities that developed after 5 years of chemical weed control were

significantly less decomposable than the other communities (40.6 % of decomposition) (Fig. 4A). In contrast, communities favoured by 5 years of tillage and 5 years of mowing had a significantly higher mass loss (48.6 % and 45.3 %, respectively) (Fig. 4A).

Communities located in mowed vineyards produced higher biomass (52 g on  $60 \times 60 \text{ cm}^2$ ) than communities managed with herbicide (23 g) and tillage (32 g) (Fig. 4B). Moreover, the total nitrogen content of the above-ground biomass was significantly higher in mowed vineyards ( $34 \text{ kg N ha}^{-1}$ ) than in chemically weeded ( $17 \text{ kg N ha}^{-1}$ ) and tilled vineyards ( $20 \text{ kg N ha}^{-1}$ ) (Fig. 4B).

$\text{N ha}^{-1}$ ) (Fig. 4C; see Supplementary data Table S5 for the detailed data).

*Functional properties of weed communities which responded to weed management practices*

Mixed linear models were computed to explain the functional properties of weed communities (CWM1, CWM2, Rao1 and Rao2) by climate, soil and weed management type. CWM1 responded to weed management type which explained 40 % of the total variance (Table 3). Compared with the other weed management types, communities developing after 5 years of chemical weeding were dominated by species with higher C:N (16.4 on average in chemically weeded communities vs. 13.5 and 13.3 in mowed and tilled communities, respectively), high lignin:N (3.2 in chemically weeded communities vs. 2 in mowed and tilled communities) and low LNC (0.3 % in chemically weeded communities vs. 1.0 % and 0.9 % in mowed and tilled communities, respectively) (Supplementary data Table S3). CWM2 and the functional diversity of communities through Rao1 and Rao2 did not respond significantly to agro-environmental filters.

*Mass loss of green organs was mostly impacted by weed management through C:N, lignin:N and LNC weighted means*

We identified the functional variables (CWM1, CWM2, Rao1 and Rao2) which were significantly related to the mass loss of green organs. CWM1 was the only functional variable selected by the models, and this variable explained 15 % of mass loss variance. The mass loss of green organs was higher when weed communities were dominated by species with

high LNC, low C:N and low lignin:N (estimate:  $-0.39 \pm 0.13$ ,  $P$ -value = 0.006).

To link mass loss, functional properties of weed communities and the agro-environmental filters identified as relevant variables by the previous models, a path analysis was performed. The selected SEM model fitted the data well (Fisher's  $C = 13.86$ , d.f. = 8 and  $P$ -value = 0.16) and explained 22 % of the mass loss of green organs (Fig. 5). Mass loss of green organs was mostly determined by CWM1 (LNC, C:N and lignin:N) as found in the previous model (Fig. 6A). The functional diversity (Rao1 and Rao2) and CWM2 did not influence the mass loss. However, Rao2 covaried positively with CWM1 (correlated error of 0.43), showing that communities dominated by species with low LNC, high C:N and high lignin:N were also composed of species with dissimilar values of leaf lignin and hemicellulose content within communities (Fig. 5). Weed management impacted the mass loss of green organs by modifying CWM1 (Fig. 6A). Indeed, chemically weeded communities were dominated by species with low quality leaves with 16 % higher C:N, 38 % higher lignin:N and 22 % lower LNC than tilled and mowed communities, resulting in 17 % lower mass loss of green organs (Supplementary data Table S3; Fig. 6A). Weed management also influenced CWM2 and Rao1. Communities managed by mowing had a lower leaf hemicellulose content (14.6 % in mowed communities vs. 15.3 % in other communities) and lower LDMC (202.6  $\text{mg g}^{-1}$  in mowed communities vs. 227.3  $\text{mg g}^{-1}$  in other communities) than communities that were managed with a shorter duration of the presence of the weeds due to more frequent disturbance (i.e. chemical weeding or tillage) (Supplementary data Table S3). Compared with chemical weeding, tillage favoured higher variability of lignin:N (43 % higher than chemically weeded communities), C:N (45 % higher) and LNC (74 % higher) within communities (Supplementary data Table S3). The between-community

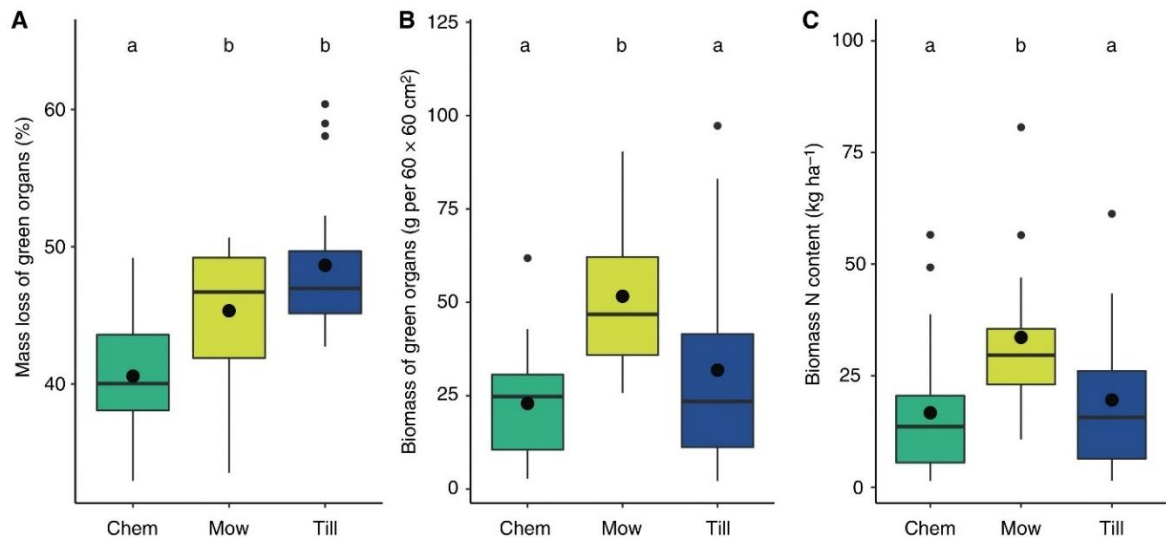


FIG. 4. (A) Mass loss of green organs according to vegetation management ( $n = 50$ ). (B) Dry above-ground biomass of green organs according to the vegetation management ( $n = 50$ ). (C) Biomass N content according to the vegetation management ( $n = 50$ ). Biomass N content was computed for biomass present on  $60 \times 60 \text{ cm}^2$  quadrats and scaled up to the hectare level. Chem, 20 communities chemically weeded for 5 years; Mow, 13 communities managed by mowing for 5 years; Till; 17 communities tilled for 5 years. Different letters indicate a significant difference (Student's  $t$ -test with  $\alpha = 0.05$ ).

TABLE 3. Community functional properties explained by climate, soil and weed management type after model selection

Community functional property	Selected models	Std. est.	Std. err.	<i>t</i>	<i>P</i>	$R^2_{\text{marg}}$	$R^2_{\text{cond}}$
<b>CWM1</b>	Weed management + (1 Vineyard)					0.40	0.64
C:N +	Chemical weeding	0.81	0.26	3.09	<b>0.003</b>		
Lignin:N +	Mowing	-0.43	0.31	-1.36	0.179		
LeafN -	Tillage	-0.57	0.25	-2.30	<b>0.026</b>		
<b>CWM2</b>	Intercept + (1 Vineyard)	-	-	-	-	0	0.40
Hemicellulose +							
LDMC +							
<b>Rao1</b>	Intercept + (1 Vineyard)	-	-	-	-	0	0.49
Lignin:N +							
C:N +							
LeafN -							
<b>Rao2</b>	Intercept + (1 Vineyard)	-	-	-	-	0	0.70
Hemicellulose +							
Lignin +							

'Weed management + (1|Vineyard)' represents the model formula with 'Weed management' as a fixed effect and (1|Vineyard) as a random effect. Significant *P*-values ( $P < 0.05$ ) are in bold. Std. est., standardized beta estimates; Std. err., standardised errors; *t*, *t*-value; *P*, *P*-value;  $R^2_{\text{marg}}$ , marginal  $R^2$ ;  $R^2_{\text{cond}}$ , conditional  $R^2$ ; CWM1, the first axis of the community-weighted means Principal Component Analysis (CWM PCA); CWM2, the second axis of the CWM PCA; Rao1, the first axis of the Rao PCA; Rao2, the second axis of the Rao PCA

The full model of each functional variable was composed of a 'weed management type' effect (chemical weeding, mowing and tillage) and pedoclimatic variables (pH + soil organic matter + silt + sand + aridity index) as fixed effects. For each model, a variable that identifies the vineyard where the communities came from was added as a random effect.

variability along CWM1 was higher in tilled vineyards (s.e. = 0.81) and mowed vineyards (s.e. = 0.84) than in vineyards managed by herbicides (s.e. = 0.33) (Fig. 6B). The SOM was the only soil variable selected by the model. Communities located in soils with high organic matter content had a higher leaf lignin and hemicellulose content (estimate: 0.49). However, its filtering effect on CWM2 did not result in significant changes in mass loss as leaf lignin and hemicellulose content were not significantly related to decomposition potential. The climate variable (aridity index) was not selected.

## DISCUSSION

### Mass loss of green organs of weed communities in Mediterranean vineyards

To our knowledge, this is the first study that has evaluated the mass loss of green organs of vineyard weeds in controlled conditions *ex situ*. We found that, on average, 45 % of the initial vegetation mass was decomposed in 2 months in optimal and standardized conditions. In contrast to most of the studies, we chose to assess the mass loss of green organs which would occur after destruction by a weed management practice (e.g. mowing). This new indicator is better adapted to agrosystems which are highly disturbed environments and, as a consequence, decomposition might occur before species senescence.

Although the green manure effect of sown cover crops has been quantified (García et al., 2018), little is known about the nitrogen content of weeds at the community level (Lindsey et al., 2013). Most of the studies quantifying the nitrogen content of weeds were done at the species level (e.g. Matos et

al., 2011; Lindsey et al., 2013; Perthame et al., 2020). Our study gave a rough estimate of the amount of nitrogen contained in the above-ground biomass of weeds that developed during the winter before the first weed management practice in Mediterranean vineyards. From the nitrogen content of this biomass sampled in 60 × 60 cm<sup>2</sup> quadrats, the extrapolation of the amount of nitrogen at the hectare level showed that weeds can represent a significant nitrogen reservoir: 22 kg N ha<sup>-1</sup> was contained in the sampled biomass on average over the 16 vineyards. Vineyard needs in terms of nitrogen are generally quite low (between 20 and 90 kg N ha<sup>-1</sup> per growing season) (Metay et al., 2014; Verdenal et al., 2021). Thus, weed mulching could contribute to meeting the vineyard's nitrogen needs. Moreover, we demonstrated that communities selected by 5 years of mowing produced more biomass and represented a higher reservoir of nitrogen (34 kg N ha<sup>-1</sup>) compared with communities selected by 5 years of chemical weeding (17 kg N ha<sup>-1</sup>) and 5 years of tillage (20 kg N ha<sup>-1</sup>). These values of biomass nitrogen content are lower than those measured by Steenwerth et al. (2016) on weed communities in Californian vineyards managed by tillage (93 kg N ha<sup>-1</sup>). This difference could be due to later sampling (in April in Steenwerth et al., 2016 vs. in March in our case). If the nitrogen content of leaves, stems and reproductive parts decreased during the vegetation season (Bumb et al. 2016), higher biomass is expected throughout the season and could explain the biomass with higher nitrogen content in the study of Steenwerth et al. (2016). However, our study did not quantify the amount of nitrogen that was released through decomposition and did not consider nitrogen immobilization in the case of low soil nitrogen availability that could happen in the field.

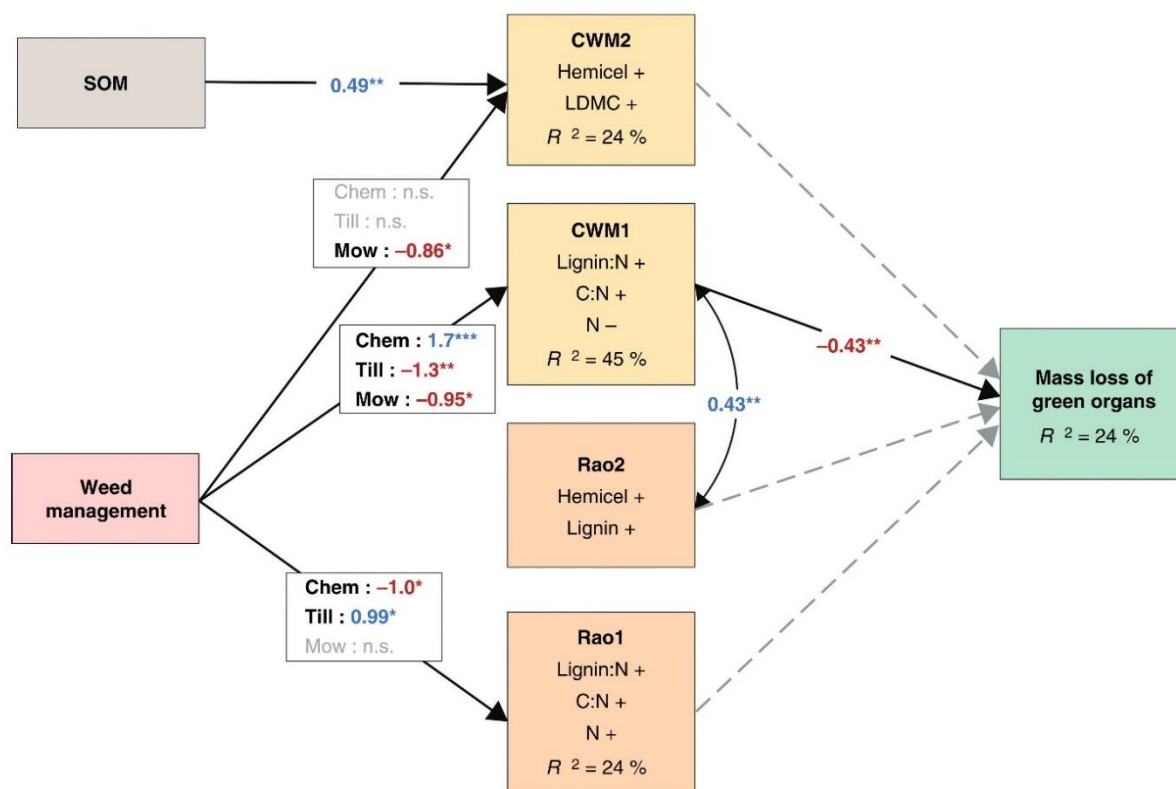


FIG. 5. Path analysis predicting the response of the mass loss of green organs of weed communities in vineyards to soil and weed management practices through their functional properties (CWM and Rao). The standardized estimates for the quantitative variables (SOM and CWM1) and the marginal means for the qualitative variable (Weed management) of each relationship are displayed. Double-headed arrows represent significantly correlated errors, while causation relationships are drawn with simple arrows. The  $R^2$  values of the response variables are indicated. Non-significant causal arrows are drawn with dashed lines. Goodness-of-fit statistics: Fisher's  $C = 13.86$ , d.f. = 8 and  $P$ -value = 0.16. SOM, soil organic matter; Chem, chemical weeding applied for 5 years; Till, 5 years of tillage practice; Mow, 5 years of mowing; CWM1 and CWM2, first and second axes of the CWM PCA, respectively; Rao1 and Rao2, first and second axes of the Rao PCA, respectively; LDMC, leaf dry matter content; C, leaf carbon content; N, leaf nitrogen content; Lignin, leaf lignin content; Lignin:N, leaf lignin to nitrogen ratio; C:N, leaf carbon to nitrogen ratio; Cel, leaf cellulose content; Hemicel, leaf hemicellulose content. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; n.s., non-significant ( $P > 0.05$ ).

#### The over-riding effect of weed management on leaf CWM and mass loss of green organs over the pedoclimate

In this study, we tested whether the functional approach could explain the effect of practices on mass loss. We hypothesized that herbicide application and tillage (i.e. disturbed environments) would select species with acquisitive strategies with a high photosynthesis rate per unit of invest dry mass (high LNC, low LDMC, low leaf fibre content and low leaf C:N) and thus high decomposability. In contrast, we hypothesized that mowing would select communities composed of species with more conservative strategies, with lower photosynthetic activity per unit of dry mass and more resistant leaves (higher LDMC, higher fibre content, lower LNC and higher leaf C:N), resulting in a lower mass loss potential through decomposition. Tilled and mowed vineyards selected communities with high decomposition potential (49 % and 45 % of mass loss, respectively), while chemical weeding favoured communities with lower decomposition potential (41 %). In the literature, the results of *in situ* experiments demonstrating weed management's influence on weed decomposition are quite scarce. In other studies, mulching was found to favour the high decomposition potential

of weeds in maize and asparagus crops (Wardle *et al.*, 1999) and teabags in vineyards (Pingel *et al.*, 2019) compared with tilled treatments. These results were related to higher microbial activities in soils, a factor that we did not consider in our *ex situ* study which could explain our contrasted results.

Our study demonstrated that weed management had a major impact on vegetation decomposition through changes in the functional properties of weeds. Five years of chemical weeding favoured communities composed of species with low-quality leaves (lower LNC, higher C:N and lignin:N) compared with tilled and mowed communities for 5 years. In contrast to our hypotheses, chemical weeding promoted communities with more conservative strategies than the other weed management types, composed of species with a low photosynthetic rate per unit of dry mass invested in the leaf and resistant leaf structure, leading to poor litter quality and low decomposability. High C:N may be due to leaf structure adaptation to decrease herbicide absorption. For instance, the presence of a thick cuticle or high wax content of leaves has been found to decrease the absorption of glyphosate (Santier and Chamel, 1992). Indeed, leaf C:N correlates positively with cuticle thickness, leading to low decomposability potential (Zukswert and Prescott, 2017).

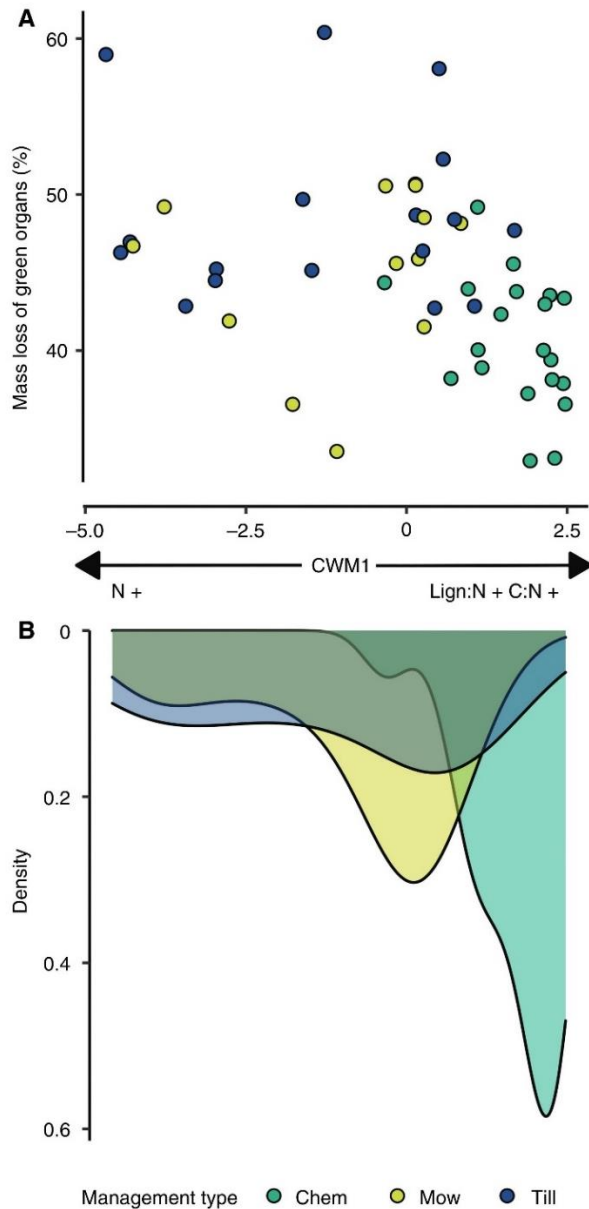


FIG. 6. (A) Mass loss of green organs as impacted by the first axis of community-weighted means PCA (CWM1) and management practice types (Chem, 5 years of chemical weeding; Mow, 5 years of mowing; Till, 5 years of tillage). CWM1 is positively correlated with the weighted means of C:N (leaf carbon to nitrogen ratio) and Lignin:N (leaf lignin to nitrogen ratio), and negatively related to leaf nitrogen content (N). (B) Distribution of the coordinates of the 50 communities along the CWM1 axis according to weed management types.

Onoda *et al.* (2012) showed that thick cuticles conferred tear resistance to leaves, slowing down the first steps of the decomposition process. Moreover, high lignin:N could be linked to lignified cell walls that strengthen the tissues and decrease the permeability of cell walls (Higuchi, 1985). Even though there is no clear evidence of this mechanism in the literature, we could hypothesize that high leaf lignin content could reduce the

absorption of glyphosate. Linkages between LNC, lignin:N and C:N and decomposition have been well established at the community level in natural and semi-natural environments, and our results are consistent with the literature (Fortunel *et al.*, 2009; Walter *et al.*, 2020; Plazas-Jiménez and Cianciaruso, 2021).

Weed management also impacted the functional diversity of the leaf traits which influenced the mass loss of green organs, i.e. lignin:N, C:N and LNC. Tillage favoured higher functional diversity of all the nitrogen-related traits, while chemical weeding was associated with lower functional diversity within communities. The reduction of within-community functional diversity by herbicides has also been highlighted in a recent study in vineyards (Hall *et al.*, 2020). Moreover, at the vineyard network scale, all the communities that were chemically weeded had similar values of CWM of lignin:N, C:N and LNC (CWM1 axis) (s.e. between chemically weeded communities = 0.33) compared with tilled (s.e. = 0.81) and mowed communities (s.e. = 0.84). This could be linked to a strong filtering effect after 5 years of herbicide use, leading to communities composed of species sharing the same strategy of investment in the leaf structure to better tolerate chemical weeding. The increase of functional diversity through tillage contrasts with the studies of Kazakou *et al.* (2016) and Hall *et al.* (2020) that demonstrated that tillage decreased functional diversity (richness and Rao) compared with weed cover in the Mediterranean and European vineyards, respectively. In our study, tilled communities were composed of species covering most of the lignin:N, C:N and leaf nitrogen variability, from acquisitive to more conservative strategies relative to the other communities of the vineyard network (Fig. 6B). In the vineyard network of this study, tilled vineyards were also more fertilized than the other vineyards: tilled vineyards received 9.2 kg N ha<sup>-1</sup> while mowed and chemically weeded communities received 6.9 and 3.2 kg N ha<sup>-1</sup> on average, respectively. Thus, tillage treatment was characterized by a high level of disturbance (2.4 tillages per year on average while chemical weeding was applied once a year maximum) but also a high potential level of resources. In grasslands, Niu *et al.* (2014) demonstrated that fertilization increased the Rao index: we assume that higher resource availability due to fertilization might enhance the coexistence of different strategies in a limited competition environment due to a higher level of nutrients and could explain higher functional diversity in tilled communities.

The relationships between community functional properties and decomposition might be explained by the presence of some dominant species. For instance, *Poa annua* was very abundant in chemically weeded communities (26 % of mean cover in chemically weeded communities and only 3 % in tilled communities and 1 % in mowed communities) and had a high leaf C:N (18.9), high leaf lignin:N (3.4) and a low LNC (2.4%). *Poa annua*'s control through chemical weeding has been reported to be problematic because of its prolific seed production and its high genetic diversity (e.g. multiple *P. annua* biotypes were found on the same golf course) (Baldwin *et al.*, 2012). However, to our knowledge, no study has yet reported leaf adaptation linked to chemical weeding tolerance. Further studies could explore these possible adaptations by measuring other traits such as the presence of cuticles or the presence and density of hairs. Moreover, legume species were absent from the chemically weeded communities while they covered 28 %

of tilled communities and 33 % of mowed communities. As nitrogen-fixing species, legume species had a high LNC (4.7 %) and low lignin:N (1.0), while other species had a lower LNC (2.9 % on average) and higher lignin:N (2.4 on average). Thus, the presence of N-fixing plants could have increased the decomposition potential of tilled and mowed communities.

Surprisingly, our results showed no effects of the pedoclimate on the functional properties that were significantly related to decomposition (CWM1, LNC, C:N and lignin:N). The reduced geographical range of this study (a circle of 40 km radius around Montpellier) might have not been sufficient for the climate to influence the functional properties related to decomposition.

#### *No direct effect of functional diversity of weed communities on the mass loss of green organs*

Although our results emphasized the impact of weighted means of traits on mass loss, we found no direct effect of within-community functional diversity measured by the Rao index on the mass loss of green organs. This contrasts with the results of recent studies that found a significant link (positive or negative) with functional diversity and decomposition (Finerty *et al.*, 2016; García-Palacios *et al.*, 2017; Migliorini and Romero, 2020; Plazas-Jiménez and Cianciaruso, 2021). Our results highlighted that the most dominant species were the main driver of mass loss, while the diversity of strategy of species co-occurring in the same community did not have a significant effect. However, the functional diversity of lignin and hemicellulose within communities covaried positively with the weighted means of lignin:N, C:N and the LNC that were significantly related to mass loss. Thus, the high diversity of lignin and hemicellulose was indirectly linked to lower mass loss of green organs even though no direct effect was found.

All in all, our study emphasized the major impact of weed management practices on the mass loss of green organs through modifying the functional properties of weed communities. Chemical weeding favoured communities with higher investment-resistant leaves (16 % higher C:N, 38 % higher lignin:N and 22 % lower LNC) which were related to lower mass loss compared with tilled and mowed communities. Functional diversity did not influence mass loss. With the likely reduction of herbicide use because of regulatory restrictions (ANSES, 2020), we can expect higher decomposition potential of future weeds, managed by tillage and mowing in vineyards and potentially a faster release of nutrients in the soil and a higher green manure service (Krishna and Mohan, 2017). Assessing the mass loss of weeds *ex situ* is one step. From an agronomic perspective, the next step would be to quantify the nutrient supplies and carbon sequestration resulting from the litter decomposition process of weeds *in situ*. Although these quantifications have been estimated for sown cover crops (Cherr *et al.*, 2006), the green manure effect of mowed weeds has been still scarcely evaluated in agrosystems.

#### SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. Figure S1: circle

of correlation of the PCA based on weed management and fertilization practices and vineyard clustering according to their PCA coordinates. Figure S2: correlation circles of agro-environmental variables of the first two axes of the PCA and the first and the third axes of the PCA. Table S1: correlation matrix of climate, soil and vegetation management and fertilization practice variables. Table S2: list of the 50 species on which traits were measured. Table S3: descriptive statistics of community-weighted means and Rao index for each trait according to the weed management type. Table S4: standardized estimated coefficients of the selected explanatory variables of the mass loss of green organs. Table S5: dry biomass, percentage of nitrogen content and nitrogen content of biomass of weeds in vineyards.

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#### CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

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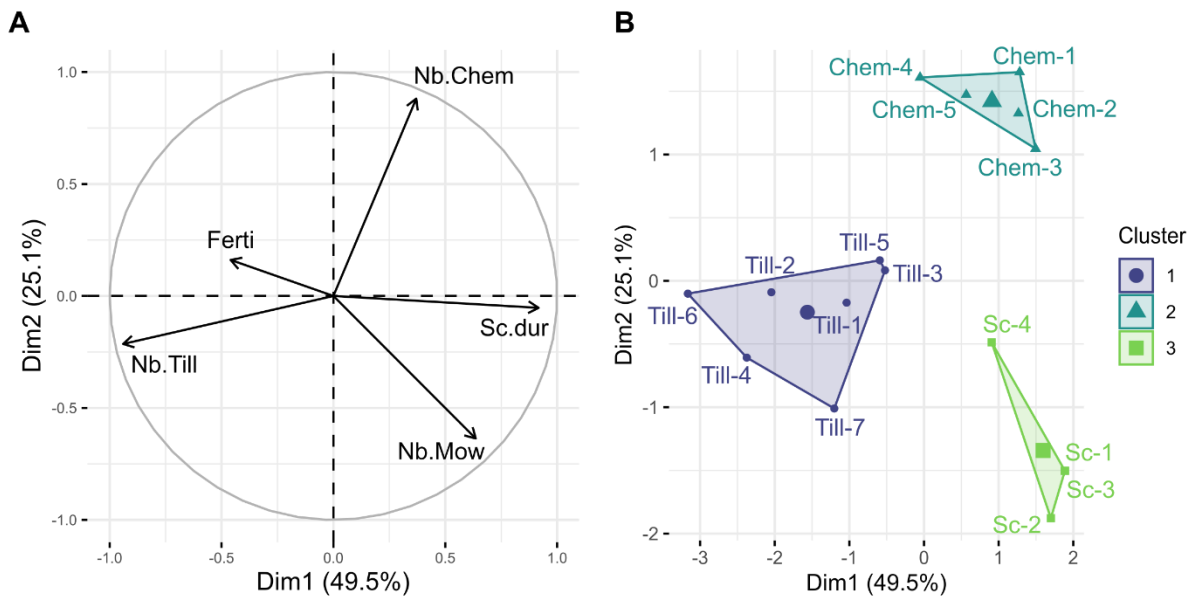
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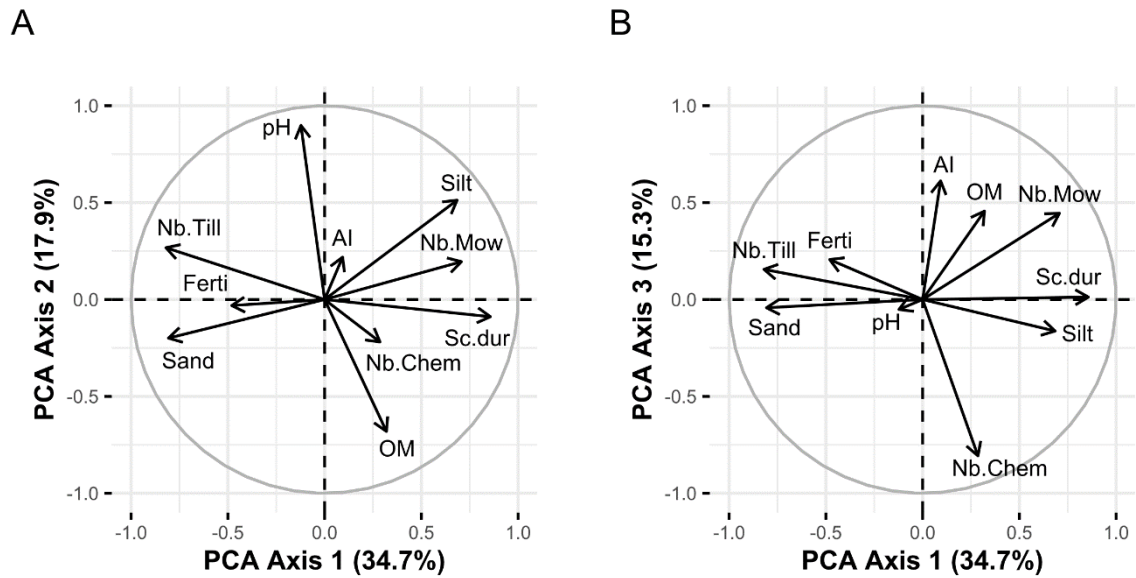
1 **SUPPLEMENTARY MATERIAL**

2



**Figure S1** Circle of correlation of the PCA based on soil management practices (A) and vineyards clustering according to their PCA coordinates (B). Cluster 1 groups 7 vineyards dominated by tillage practice and higher nitrogen input than the other vineyards (Till), cluster 2 includes 4 long spontaneous cover-cropped vineyards managed by mowing (Sc), cluster 3 gathers the 5 chemically weeded vineyards (Chem). All the variables were averaged over 2015 to 2020 to consider cultural history : Nb.Chem, the number of chemical weeding of inter-rows; Nb.Till, the number of tillage of inter-rows; Nb.Mow, the number of mowing of inter-rows; Sc.dur, the annual longest period of time between two weed destructions by tillage or chemical weeding; Ferti, the annual nitrogen fertilisation input.

3



**Figure S2** Correlation circles of agro-environmental variables of the first two axes of the PCA (A) and the first and the third axes of the PCA (B). The percentage of the data variability explained by each axis is indicated in brackets. OM, Organic Matter; AI, Aridity Index; Sc.dur, maximum spontaneous cover duration within a year; Nb.Till, number of tillage of inter-rows within a year; Nb.Mow, number of mowing of inter-rows within a year; Nb.Chem, number of chemical weeding of inter-rows within a year; Ferti, Nitrogen supply within a year.

1

2 Covariations between soil management, soil characteristics and climate were investigated by  
 3 performing a PCA including all the explaining variables. The first three axes of the PCA of agro-  
 4 environmental factors explained 67.9% of vineyard variability [**Supplementary Information**  
 5 **Figure S1**]. The first axis explained 34.7% of data variance and described well the interaction  
 6 between soil texture and tillage versus mowing practices [**Supplementary Information Figure**  
 7 **S1**]. This axis opposed vineyards with long-lasting and frequently mown spontaneous vegetation  
 8 located in silty soils against frequently tilled vineyards located in sandy soils. The second axis  
 9 explained 17.9% of agro-environmental conditions and was driven by soil characteristics. It  
 10 discriminated against alkaline soils with low organic matter versus acidic soils with high organic  
 11 matter. The third axis accounted for 15.3% of data variation and described chemical weeding and  
 12 climate covariations. It opposed chemically weeded vineyards with low aridity index and organic  
 13 matter content to vineyards without chemical weeding (mowed inter-rows) with soils with high  
 14 organic matter content and high aridity index. We estimated the significance of the correlations  
 15 between the explaining variables (soil, climate and soil management practices) (Pearson  
 16 correlation test with p-values corrected using the Holm method) [**Supplementary Information**  
 17 **Table S1**]. Only 3 correlations were significant : a negative correlation between silty and sandy

- 1 soils (correlation coefficient : -0.77), a negative correlation between sandy soils and mowing
- 2 (correlation coefficient : -0.75) and a negative correlation between tillage and the maximum
- 3 duration of spontaneous cover cropping (correlation coefficient -0.89).

1

**Table S1** Correlation matrix of climate (AI, Aridity Index), soil (SOM, Soil organic Matter; pH; Sand; Silt) and soil management practice variables (Sc.dur, the annual longest pe between two weed destructions; Nb.Till, the annual number of tillage of inter-rows; Nb.Mow, the annual number of mowing of inter-rows; Nb.Chem, annual number of chemical weeding of inter-rows; Ferti, fertilisation input). The significant coefficients corrected for multiple testing bias using the Holm method are in bold. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ; no asterisks, non-significant ( $p > 0.05$ ).

	<b>SOM</b>	<b>pH</b>	<b>Sand</b>	<b>Silt</b>	<b>AI</b>	<b>Sc.dur</b>	<b>Nb.Till</b>	<b>Nb.Mow</b>	<b>Nb.Chem</b>	<b>Ferti</b>
<b>SOM</b>	1,00									
<b>pH</b>	-0,66	1,00								
<b>Sand</b>	-0,38	0,36	1,00							
<b>Silt</b>	0,09	-0,14	<b>-0,77*</b>	1,00						
<b>AI</b>	0,08	0,01	0,17	-0,12	1,00					
<b>Sc.dur</b>	0,31	-0,30	-0,50	0,36	0,07	1,00				
<b>Nb.Till</b>	-0,23	0,37	0,48	-0,31	-0,08	<b>-0,89***</b>	1,00			
<b>Nb.Mow</b>	0,41	-0,61	<b>-0,75*</b>	0,54	0,09	0,59	-0,50	1,00		
<b>Nb.Chem</b>	0,03	-0,29	-0,09	0,11	-0,05	0,01	-0,40	-0,09	1,00	
<b>Ferti</b>	0,27	-0,03	0,13	-0,19	-0,13	-0,31	0,28	-0,36	0,02	1,00

2

**Table S2** Detailed list of the species that had measured trait values and the main weed management practices of the vineyards where they were sampled. Chem, Chemical weeding; Till, tillage; Sc, Spontaneous cover cropping.

Species	Chem	Till	Sc
<i>Anisantha madritensis</i>			X
<i>Anisantha sterilis</i>		X	
<i>Avena sterilis</i>			X
<i>Calendula arvensis</i>		X	
<i>Cardamine hirsuta</i>			X
<i>Cerastium glomeratum</i>	X		
<i>Convolvulus arvensis</i>		X	
<i>Crepis foetida</i>		X	
<i>Crepis pulchra</i>		X	
<i>Crepis sancta</i>	X	X	X
<i>Cynodon dactylon</i>		X	
<i>Daucus carota</i>		X	
<i>Diplotaxis eruroides</i>		X	
<i>Erigeron canadensis</i>	X		
<i>Erigeron sumatrensis</i>	X		
<i>Erodium cicutarium</i>	X		X
<i>Euphorbia prostrata</i>			X
<i>Galium parisiense</i>			X
<i>Geranium molle</i>			X
<i>Geranium rotundifolium</i>	X	X	
<i>Helminthotheca echioides</i>			X
<i>Hirschfeldia incana</i>		X	
<i>Hordeum murinum</i>			X
<i>Lactuca serriola</i>		X	
<i>Lamium amplexicaule</i>		X	
<i>Lepidium draba</i>		X	
<i>Lolium rigidum</i>		X	X
<i>Malva sylvestris</i>	X		
<i>Medicago minima</i>		X	
<i>Medicago orbicularis</i>		X	
<i>Medicago polymorpha</i>		X	X
<i>Plantago lanceolata</i>			X
<i>Poa annua</i>	X	X	X
<i>Poa infirma</i>	X		
<i>Rumex crispus</i>			X
<i>Rumex pulcher</i>		X	
<i>Sagina apetala</i>	X		
<i>Scabiosa atropurpurea var. maritima</i>		X	X
<i>Scorpiurus subvillosus</i>			X
<i>Senecio vulgaris</i>	X		
<i>Sherardia arvensis</i>		X	
<i>Solanum sp</i>			X
<i>Sonchus asper</i>	X		

<i>Sonchus oleraceus</i>	X		
<i>Stellaria media</i>		X	
<i>Stellaria pallida</i>	X		
<i>Trifolium lappaceum</i>			X
<i>Trifolium spumosum</i>		X	
<i>Veronica persica</i>	X		
<i>Vicia hybrida</i>			X
<i>Vulpia ciliata</i>			X

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**Table S3** Descriptive statistics of Community Weighed Means and Rao index for each trait according to the weed management type

Functional properties		Units	Chemical weeding mean +/- sd (min - max)	Spontaneous cover crop mean +/- sd (min - max)	Tillage mean +/- sd (min - max)
Community Weighed Means					
	Leaf C content	(%)	40.89 +/- 0.55 (40.07 - 42.16)	42.07 +/- 1.43 (40.13 - 44.64)	42.26 +/- 1.89 (39.01 - 44.77)
	Leaf N content	(%)	2.78 +/- 0.34 (2.38 - 3.59)	3.52 +/- 0.7 (2.85 - 4.78)	3.67 +/- 0.81 (2.42 - 4.99)
	Leaf C:N	-	16.39 +/- 1.62 (13.69 - 18.79)	13.46 +/- 1.9 (10.11 - 15.64)	13.26 +/- 2.59 (9.17 - 17.4)
	Leaf cellulose	(%)	17.02 +/- 1.78 (10.54 - 18.56)	15.15 +/- 2.3 (13.21 - 20.11)	14.49 +/- 1.52 (12.93 - 18.42)
	Leaf hemicellulose	(%)	16.19 +/- 2.81 (10.35 - 19.12)	14.6 +/- 3.68 (10.54 - 22.77)	14.3 +/- 2.29 (9.21 - 19.46)
	LDMC	mg.g <sup>-1</sup>	231.81 +/- 27.73 (176.35 - 270.56)	202.6 +/- 27.74 (165.71 - 245.43)	222.73 +/- 26.18 (171.68 - 254.29)
	Lignin	(%)	7.42 +/- 0.84 (6.01 - 10.06)	6.13 +/- 0.91 (4.66 - 7.69)	6 +/- 1.52 (4.43 - 9.79)
	Lignin:N	-	3.15 +/- 0.26 (2.36 - 3.68)	1.99 +/- 0.52 (1.02 - 2.56)	2 +/- 0.79 (0.91 - 3.53)
	Rao index Leaf C content	(%)	0.25 +/- 0.25 (0 - 0.99)	0.97 +/- 0.46 (0.42 - 1.97)	0.95 +/- 0.77 (0.29 - 3.28)
	Leaf N content	(%)	0.3 +/- 0.39 (0 - 1.35)	0.99 +/- 0.32 (0.52 - 1.52)	0.91 +/- 0.61 (0.11 - 2.27)
	Leaf C:N	-	0.34 +/- 0.27 (0 - 1.03)	0.47 +/- 0.14 (0.29 - 0.67)	0.62 +/- 0.53 (0.06 - 2.3)
	Leaf cellulose	(%)	0.43 +/- 0.21 (0 - 0.76)	0.51 +/- 0.36 (0.22 - 1.23)	0.69 +/- 0.54 (0.05 - 1.66)
	Leaf hemicellulose	(%)	0.51 +/- 0.39 (0 - 1.76)	0.48 +/- 0.28 (0.19 - 1)	0.72 +/- 0.69 (0.1 - 2.18)
	LDMC	mg.g <sup>-1</sup>	0.78 +/- 0.55 (0 - 1.66)	0.59 +/- 0.25 (0.21 - 1.01)	0.63 +/- 0.42 (0.11 - 1.59)
	Lignin	(%)	0.58 +/- 0.5 (0 - 1.79)	0.62 +/- 0.54 (0.08 - 1.86)	0.96 +/- 0.99 (0.03 - 3.78)
	Lignin:N	-	0.46 +/- 0.34 (0 - 1.1)	0.59 +/- 0.2 (0.31 - 0.98)	0.81 +/- 0.54 (0.11 - 2.2)



Table S4 Standardised estimated coefficients of the selected explaining variables of the mass loss of green organs (50 communities). Significant p-value ( $p < 0.05$ ) are in bold. Std. est.; standardised estimates; Std. err., standardised errors; t, t-value; p, p-value.

<b>Mass loss of green organs</b>				
<b>Predictors</b>	<b>Std. est.</b>	<b>Std. err.</b>	<b>t</b>	<b>p</b>
Chemical weeding	-0.66	0.19	36.02	<0.001
Spontaneous cover cropping	0.79	0.30	2.65	0.011
Tillage	1.33	0.27	4.86	<0.001
Observations		50		
R2 / R2 adjusted		0.339 / 0.310		

**Table S5** Dry biomass, percentage and biomass nitrogen content composed of spontaneous vegetation in vineyards

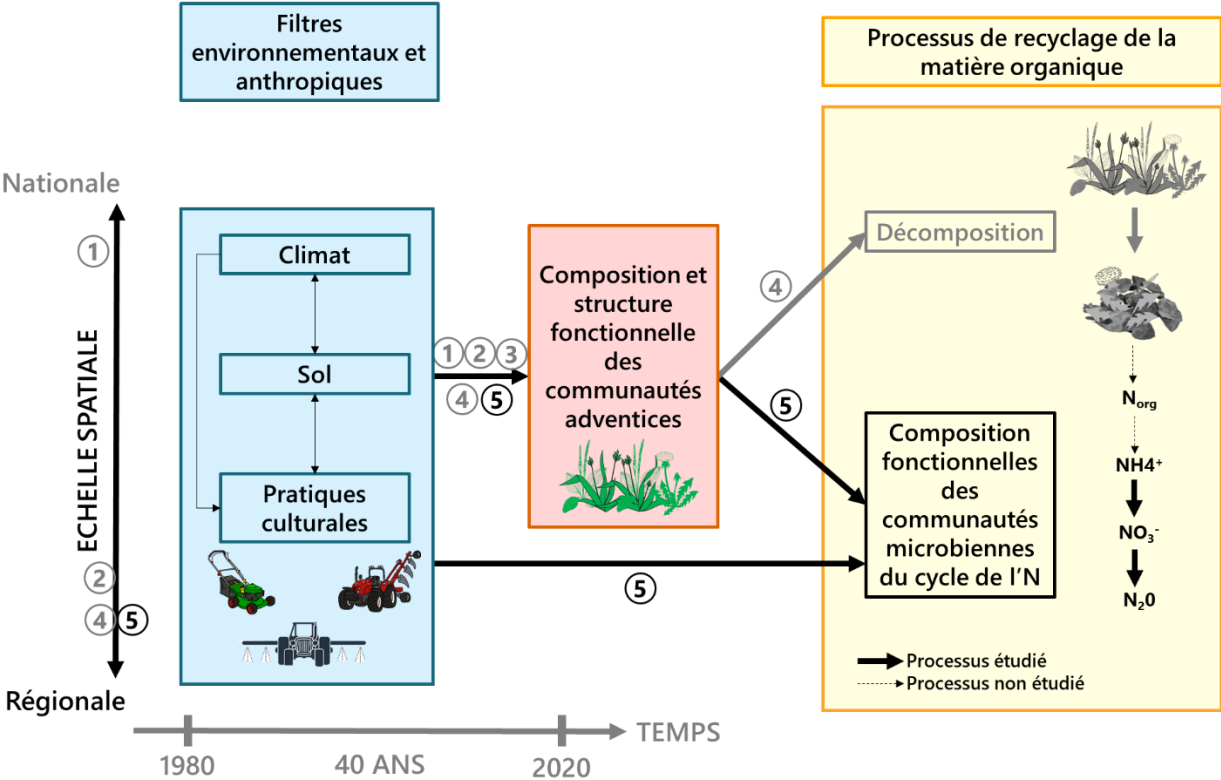
<b>Vineyard</b>	<b>Dry biomass (g) collected on 60x60 cm<sup>2</sup> quadrats</b>	<b>% N content</b>	<b>N content (kg per hectare)</b>
Chem-1	14.6	1.7	6.6
Chem-2	5.7	2.0	3.3
Chem-3	44.6	3.2	40.3
Chem-4	24.6	2.0	14.0
Chem-5	25.3	2.7	19.2
Sc-1	35.9	2.6	26.7
Sc-2	90.4	1.3	32.3
Sc-3	39.6	1.9	21.1
Sc-4	69.7	2.7	53.3
Till-1	18.9	2.0	11.0
Till-2	54.4	3.0	46.6
Till-3	17.5	3.6	17.3
Till-4	6.1	2.1	3.4
Till-5	69.1	1.5	26.0
Till-6	72.7	1.9	38.3
Till-7	13.3	2.8	10.8
Mean	33.4	2.4	22.1



# Chapitre 5 – Impact of weed management on weed communities and soil microbial nitrogen-cycling properties in French Mediterranean vineyards using a trait-based approach

Bopp, M.-C., Kazakou, E., Fried, G., Metay, A., Fort, Moinet, G., F., Fromin, N., Buatois, B., De Deyn, G., Lammert, B., Zwetsloot, M.

Article en cours de préparation





## **Présentation du chapitre**

Ce chapitre est basé sur un jeu de données de relevés floristiques (n=60 communautés) de la région du Montpelliérais (15 parcelles de vignes), observés en mars 2020. Une série de traits aériens et racinaires a été mesurée dans les parcelles de vignes ainsi que des potentiels d'activités microbiennes qui renseignent la biomasse microbienne du sol et les abondances des microorganismes nitrifiants et dénitrifiants. **L'objectif de cette étude est de comprendre les effets indirects des pratiques de gestion, de fertilisation et des conditions pédoclimatiques sur les potentiels d'activités microbiennes via leurs effets sur les propriétés fonctionnelles aériennes et racinaires des communautés adventices viticoles.**

**Les hypothèses de cette étude sont les suivantes:**

- (i) Les communautés adventices issues de parcelles viticoles désherbées chimiquement et travaillées sont des communautés à stratégies d'acquisition de ressources favorisant une abondance de microorganismes nitrifiants, dénitrifiants et une biomasse microbienne élevées,
- (ii) Les communautés adventices issues de parcelles viticoles tondues sont des communautés à stratégies plus conservatrices que les communautés issues de parcelles désherbées chimiquement et travaillées, favorisant une abondance de microorganismes nitrifiants, dénitrifiants et biomasse microbienne plus faibles.

Trois résultats clés sont obtenus dans cette étude (Figure 22). Premièrement, la gestion des adventices affecte de manière significative les stratégies souterraines des adventices: l'application d'herbicides pendant au moins cinq ans filtre les communautés adventices caractérisées par des stratégies « *do-it-yourself* », c'est-à-dire d'exploration des ressources du sol via de longues racines à faible masse sèche (« Specific Root length » élevé, SRL, soit le rapport longueur sur masse sèche des racines), tandis que le travail du sol et la tonte sélectionnent des communautés adventices dont la stratégie d'acquisition de ressources repose sur la collaboration avec les champignons mycorhiziens. Deuxièmement, l'abondance relative des microorganismes nitrifiants est déterminée par le SRL des communautés adventices (les facteurs pédoclimatiques et agronomiques n'ont pas été sélectionnés dans les modèles). En revanche, les caractéristiques abiotiques du sol (pH et texture) sont les principaux facteurs déterminant la biomasse

microbienne (mesurée par la *substrate-induced respiration*, SIR) et l'abondance relative des microorganismes dénitrifiants. Dans une moindre mesure que les caractéristiques abiotiques du sol, la gestion a également une influence sur la biomasse microbienne du sol: les communautés adventices issues de parcelles tondues ont une biomasse microbienne 58% plus élevée que les communautés issues de parcelles désherbées chimiquement.

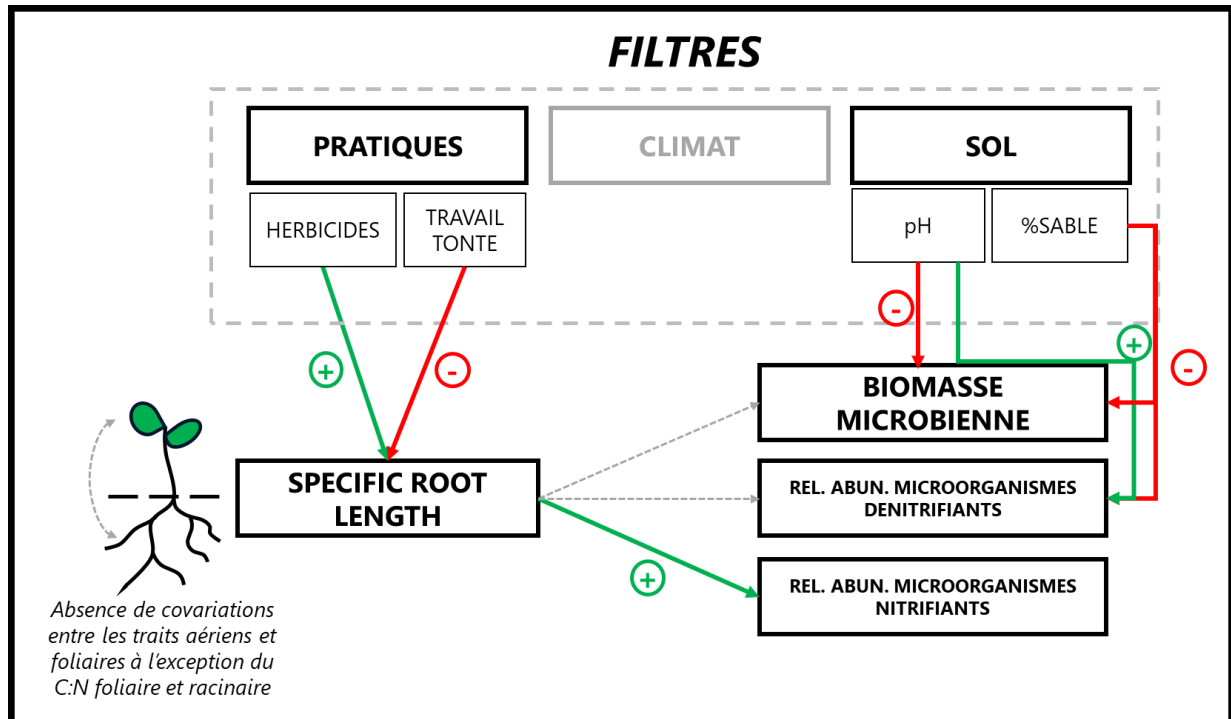


Figure 22 Résumé graphique du chapitre 5. Premièrement, les propriétés fonctionnelles aériennes et souterraines des communautés adventices varient indépendamment à l'exception du C:N des feuilles et des racines qui covarient positivement. Deuxièmement, la gestion des adventices est le principal moteur de la longueur spécifique des racines (« Specific root length ») à l'échelle de la communauté alors que les caractéristiques abiotiques du sol ont peu d'effet et que le climat n'a aucun effet sur les propriétés fonctionnelles des communautés adventices. Troisièmement, la longueur spécifique des racines est positivement corrélée avec l'abondance relative des microorganismes nitrifiants alors qu'aucune propriété fonctionnelle des communautés adventices n'est corrélée de manière significative avec la biomasse microbienne ou avec l'abondance relative des microorganismes dénitrifiants. Quatrièmement, la biomasse microbienne et l'abondance relative des microorganismes dénitrifiants sont expliquées par le pH et le pourcentage de sable dans les sols. Les flèches en gras représentent des corrélations significatives et les flèches en pointillés signifient l'absence de corrélation. La couleur des flèches est associée aux signes des relations : verte, positive ; rouge, négative.

## **TITLE**

# **Impact of weed management on weed communities and soil microbial nitrogen-cycling properties in French Mediterranean vineyards using a trait-based approach**

## **ABSTRACT**

Nitrogen (N) availability is key in sustaining crop productivity in agroecosystems and is largely determined by soil microbial processes such as nitrification and denitrification. Trait-based approaches offer a useful tool to better understand how plant-microbe interactions drive soil N cycling in agroecosystems. Using a network of 15 Mediterranean vineyards, we quantified the effect of five years of different weed management practices (chemical weeding, tillage, mowing) on the aboveground and belowground functional properties of weed communities and the soil microbial nitrogen-cycling properties. The functional properties of microbial communities were quantified using soil substrate-induced respiration (SIR) representing microbial biomass and potential nitrifying and denitrifying enzyme activities to SIR ratio (PNEA:SIR, PDEA:SIR) expressing the abundance of nitrifiers and denitrifiers relative to soil heterotroph microbial communities, respectively. Three key findings were obtained in this study. First, we demonstrated that the aboveground and belowground functional properties of weed communities were uncoupled except for leaf and root C:N, which were positively correlated. Second, management significantly affected weed belowground strategies: the specific root length (SRL) of the tilled and mowed weed communities were 30% and 44% lower than the herbicide-treated weed communities, suggesting a change from collaboration with mycorrhizal fungi towards do-it-yourself strategies. Third, abiotic soil characteristics (pH and sandy texture) were the main drivers of the soil microbial biomass (SIR) and the relative abundance of denitrifiers within soil heterotroph microbial communities (PDEA:SIR). In contrast, SRL was the sole driver of the relative abundance of nitrifiers (PNEA:SIR) according to the best models tested. Weed communities with do-it-yourself strategies were associated with soils with higher relative abundances of nitrifiers. To a lesser extent than soil abiotic characteristics, management also impacted soil microbial biomass (SIR): mowed weed communities had 58% higher SIR compared



to chemically weeded communities. Thus, the current trend to replace chemical weeding by mowing the inter-rows in French Mediterranean vineyards (*i.e.* the free space between vine rows) might favour higher microbial biomass and belowground collaborative weed communities. Trait-based approaches could help define more extensive weed management in the future that would improve soil processes in agroecosystems.

## **KEYWORDS**

Weed communities, Mediterranean vineyards, trait-based approach, root traits, substrate-induced respiration, nitrifying enzyme activity, denitrifying enzyme activity

# INTRODUCTION

Plant-microbe interactions have a big impact on nitrogen (N) availability in agroecosystems and thereby provide a key ecosystem service (Drinkwater and Snapp, 2007; Henneron et al., 2020). In agroecosystems, weed communities represent a large part of spontaneously growing plant biodiversity (Mahaut et al., 2020), especially in perennial agroecosystems. Mediterranean vineyards are particularly susceptible to erosion risks and organic matter loss, especially due to rainfall intensity, low amendment input, inter-row spacing, and intensity of weed management practices (Garcia et al., 2018; Novara et al., 2018; Romero et al., 2022). In vineyards, growing evidence suggests that weed communities are involved in many agroecosystem processes like soil stabilisation (Garcia et al., 2019) or soil water replenishment (Garcia et al., 2020) but how they influence nitrogen cycle is yet to be determined. Weed management practices are diversifying and based on the combinations of three main practices (Fernández-Mena et al., 2021): tillage, chemical weed control and mowing. How weed management impacts weed-microorganism interactions is unknown.

In addition to mineralization, nitrogen availability is driven by two major microbial processes: nitrification and denitrification. Nitrification is a two-step aerobic process performed by autotrophic microbes (Robertson, 1982) while denitrification is an anaerobic process that reduces nitrate and nitrite to gaseous forms of N by microbial heterotrophs (Skiba, 2008). Nitrification is driven by soil ammonium concentrations and soil water content (Koskinen and Keeney, 1982; Zumft and Körner, 1997) while denitrification is dependent on nitrate concentration, pH, soil organic matter and soil water content (Skiba, 2008). The measure of these two processes in optimal conditions (Potential Nitrifying Enzyme Activity, PNEA, and Potential Denitrifying Enzyme Activity, PDEA) can be considered as microbial functional properties at the community level (Grigulis et al., 2013; Pommier et al., 2018). Plant communities can significantly influence both nitrifiers and denitrifiers microbial communities through many mechanisms including depletion of microbial substrates (Cantarel et al., 2015; Grigulis et al., 2013; Laughlin, 2011; Nuñez et al., 2022), soil water retention (Abalos et al., 2019) or the release of root exudates used as a carbon source by soil microorganisms (Li et al., 2021; Moreau et al., 2019).

Trait-based approaches offer a useful framework to better understand the interactions between plant and microbial communities that drive N cycling in soil (Bardgett et al. 2014, Abalos et al. 2019). Indeed, exploring trait values of plant communities allow to describe their economic strategy and their capacity to modify their environment (Lavorel and Garnier, 2002). As resources are limited, a fundamental trade-off exists between rapid acquisition of resources and efficient conservation of resources (Wright et al., 2004). Acquisitive species are characterised by high metabolic rate, high photosynthesising leaf area and specific leaf area (SLA), high leaf N content and short organ lifespan while conservative species invest in higher leaf tissue density, lower photosynthesising leaf area and SLA, and longer organ lifespan (Reich, 2014; Wright et al., 2004). Recently, the root economics space was defined by two main axes (Bergmann et al., 2020): (i) a conservation gradient from acquisitive root systems with high root nitrogen content to conservative root systems with high root tissue density and (ii) a collaboration gradient from do-it-yourself root systems with high specific root length (SRL) to outsourcing root systems with high root diameter, based on collaboration with mycorrhizal fungi. Trait-based studies have demonstrated that linking nitrification and denitrification to plant functional properties is not straightforward, quantifying little (Cantarel et al., 2015) or strong (Laughlin, 2011) relations with aboveground traits as well as little (Orwin et al., 2010) or strong (Cantarel et al. 2015) links with root traits. Acquisitive plant species have been associated with higher nitrification potential (Cantarel et al., 2015; Laughlin, 2011; Orwin et al., 2010) due to faster N cycling and reduced N immobilisation in microbial biomass (Henneron et al., 2020). Trait relations with denitrification potential are less consistent across studies. Some studies demonstrated that conservative species had negative impacts on denitrification potential (see Abalos et al. 2019 for a review) but few studies also found positive effects (Cantarel et al., 2015; Legay et al., 2020).

All the studies exploring the interactions between the functional properties of plant and microbial communities involved in N cycling were based on species occurring in natural or semi-natural ecosystems (*e.g.* grasslands, understorey vegetation of forests) (*e.g.* Orwin et al. 2010, Laughlin 2011). To our knowledge, no study has yet included the effect of soil and weed management on plant and microorganism community interactions in more intensively managed ecosystems. These management practices can impact the functional properties of the microbial community directly or indirectly through its impact on weed functional properties. A recent meta-analysis quantified that no-tillage practice directly increased PDEA by 66% by favouring

more anaerobic conditions with higher water-filled pore space due to higher soil moisture and bulk density (Wang & Zou, 2020). Tillage negatively influenced SIR due to larger organic matter input in no-tilled systems (Andrade et al., 2002; Hashimi et al., 2020). Studies show contrasting effects of mowing on PDEA and PNEA. Compared to unmown and unmanaged environments, mowing has been shown to have no significant impact on PNEA (Robson et al., 2007; Song et al., 2022) and PDEA (Song et al., 2022) or positive effect on PDEA due to higher soil temperatures after mowing operation (Robson et al., 2007; Zhang et al., 2018). A recent meta-analysis demonstrated that glyphosate enhanced SIR in short term but then reduced it in the longer term (Nguyen et al., 2016). Indeed, the addition of glyphosate provides metabolizable carbon, nitrogen and phosphorus and triggered microbial growth and respiration shortly after its application (Duke et al., 2012). To our knowledge, no study has yet explored the impact of chemical control on PNEA and PDEA.

Recent studies demonstrated that weed management can also shape weed community composition and associated economic strategies in vineyards (Bopp et al., 2022; Hall et al., 2020; MacLaren et al., 2019; Mainardis et al., 2020), which could indirectly impact soil N cycling. For instance, mowing favoured more conservative weed communities, including higher abundance of perennial species, higher stature, lower SLA and higher leaf dry matter content (LDMC) (Bopp et al., 2022b; Fried et al., 2022; Guerra et al., 2021; Hall et al., 2020; Kazakou et al., 2016; Mainardis et al., 2020). In contrast, tillage and chemical weeding favoured more acquisitive communities composed of more annual species with higher SLA and lower LDMC (Bopp et al., 2022b; Fried et al., 2022; Hall et al., 2020). While the aboveground strategies of weed communities have been studied, studies on root responses to intensive management are lacking. Yet, aboveground and belowground strategies of weed communities might be decoupled (*i.e.* root traits might not covary with aboveground traits) (Mahaut et al., 2020). Considering that root traits play key roles in ecosystem functioning in the natural or semi-natural environment (Bardgett et al., 2014; Freschet et al., 2021; Laliberté, 2016) and particularly in soil N cycling (Abalos et al., 2019), there is a growing need to understand how management influences the belowground functional properties of weeds.

In this study, we quantified the effect of five years of different weed management practices (chemical weeding, tillage with high fertilisation, mowing with amendment) on the functional

properties of weed and microbial communities in 15 Mediterranean vineyards, near Montpellier, France. We hypothesised that tillage and chemical weeding would filter more acquisitive weed communities than mowing and would favour higher microbial biomass (high SIR) and relative abundance of nitrifiers (PNEA:SIR) and denitrifiers (PDEA:SIR) due to faster N cycling. First, we characterised the covariations of aboveground and belowground functional properties of weed communities (Figure 1, arrow 1). Second, we investigated how weed community functional properties responded to management, soil abiotic characteristics and climate (Figure 1, arrow 2). Then, we tested how the aboveground and belowground functional properties of weed communities related to the functional properties of soil microorganisms (PNEA: SIR, PDEA: SIR, SIR) (Figure 1, arrow 3). Finally, we tested the response of N-related microbial functional properties (PNEA: SIR, PDEA: SIR, SIR) to climate, soil abiotic characteristics, management and weed above and belowground functional properties (Figure 1, arrows 4).

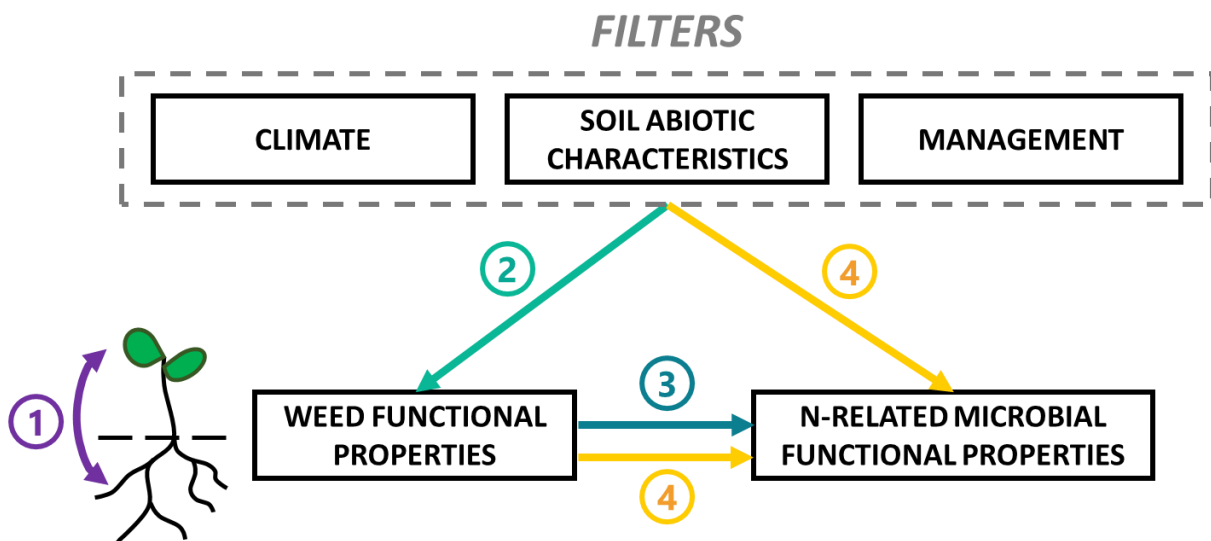


Figure 1 Analytical framework linking agroenvironmental filters (climate, soil abiotic characteristics and management) to weed and nitrogen-related microbial functional properties. First, we examined how aboveground and belowground coupled for weeds at the community level (arrow 1). Second, we explored how filters impacted weed functional properties at the community level (arrow 2). Third, we investigated how weed functional properties related to N-related microbial functional properties (arrow 3). Fourth, we tested the response of N-related microbial functional properties to climate, soil abiotic characteristics, management and weed functional properties (arrows 4).

# MATERIALS AND METHODS

## 1. Climate and soil characterisation of the vineyard network

We studied a network composed by 15 vineyards located around Montpellier, South France (Figure 2, see three examples in Figure 3). The climate is warm with a mean annual temperature of 14.8°C and irregular rainfall (801 mm with most of the rainfall occurring in Autumn) (Table S1). The northern vineyards of the network had the lowest mean annual temperatures (minimum near Ganges: 13.7°C) and higher rainfall (maximum near Ganges: 923 mm) (Figure 2). In contrast, vineyards near the Mediterranean Sea had the highest mean annual temperatures (maximum near Lunel: 15.9°C) and the lowest rainfall (minimum near Pézenas: 554 mm) (Figure 2).

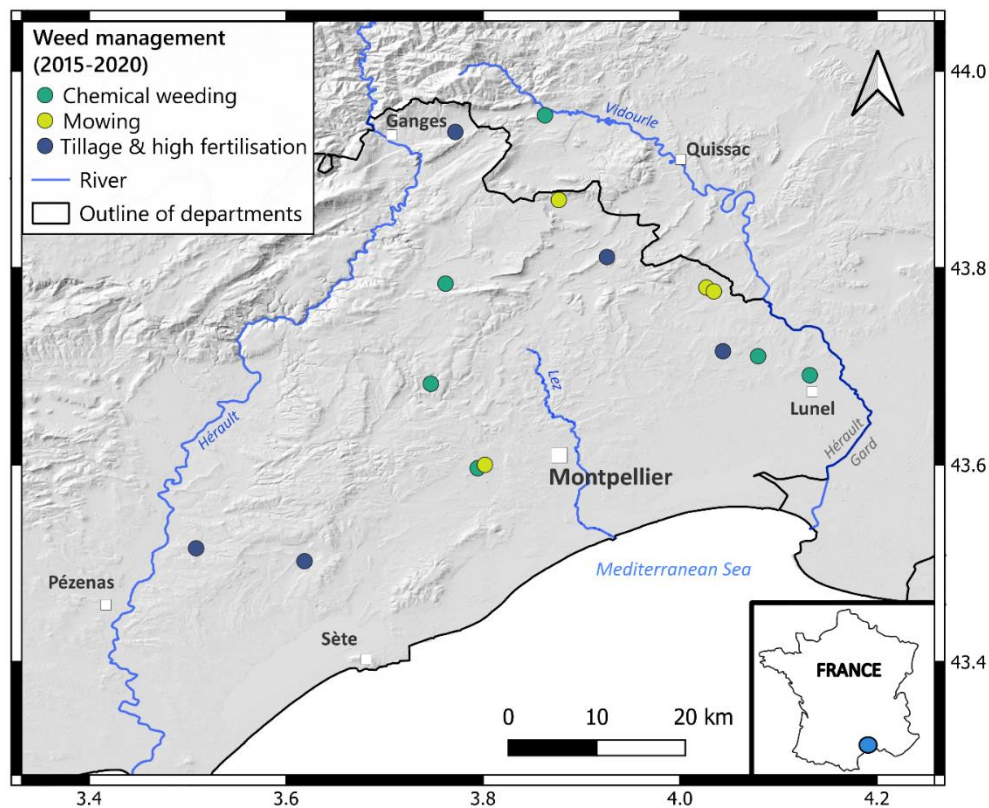


Figure 2 Weed management of the 15 vineyards nearby Montpellier, France. Each dot is a vineyard whose colour refers to weed management applied by the farmers: green, 5 years of chemical weeding; light green, 5 years of mowing and long period of weed cover presence; blue, 5 years of tillage on the inter-rows and chemical weeding on the rows with high fertilisation input. The blue lines represent the main rivers of the region. The dark lines represent the outlines of the departments.

Vineyard soils were sampled from the 0–10 cm topsoil layer within the inter-rows of the vineyards (*i.e.* the free space between the rows of the vines). Ten samples were collected in different inter-rows within the same vineyard and mixed to get one sample per vineyard. Soil textures ranged from sand-loamy soils around Montpellier (maximum: 70% of sands) to clay-loamy soils in the northern part of the network (maximum 34% of clay) (Table S1). Vineyards located nearby the coastline of the Mediterranean Sea had loamy and clay loamy soils. The soil samples had 2% of organic matter content on average (2%) with high variability across vineyard soils (from 0.7% to 5%) (Table S1).

## **2. Weed management and fertilisation practices within the vineyard network**

Weed management and fertilisation practices from 2015 to 2020 were collected from interviews in June 2020. The questionnaire was divided into three sections: (i) farm characteristics (area, wine valorisation, labels), (ii) vineyard characteristics (topography, vine density, grape variety, fertilisation, manure, irrigation) and (iii) the type of weed management practices of rows and inter-rows from 2015 to 2020 (chemical weeding, tillage and mowing). From these raw data, we selected the variables that described the level of disturbance and nutrient resource management and averaged them over 2015-2020 to consider the possible effect of management history on both plant and microbial communities (Gulden et al., 2015). First, the frequency and the type of disturbance were described by six variables: the number of chemical weeding and tillage of rows and inter-rows, the number of mowing of inter-rows and the annual longest period of weed presence between tillage or chemical weeding events. Nutrient resource management was characterised by two variables: mineral NPK annual inputs and annual inputs of vinasse (*i.e.* residuum after wort distillation). To consider covariations between these variables, we performed a Principal Component Analysis (PCA) (Figure S1). Then, hierarchical clustering was used based on the coordinates of the 15 vineyards in the PCA to identify groups of vineyards with similar weed management practices. Vineyard management was classified into three groups (Figure S1, Figure 3): (i) vineyards with inter-rows managed by tillage and rows managed by chemical with higher fertilisation than the other vineyards ('Till&N', five vineyards), (ii) vineyards managed by chemical weeding on both rows and inter-rows ('Chem', six vineyards)

and (iii) vineyards managed by mowing of inter-rows with a long period of weed cover presence and inputs of vinasse ('Mow', four vineyards). We checked the dependency of pedoclimate characteristics and management groups. The group 'Mow' had a higher soil organic matter content (2.7%) than the other groups (1.6% for 'Till&N' vineyards and 1.7% for 'Chem' vineyards). 'Till&N' vineyards had a more alkaline soil (8.5) than 'Chem' (8.2) and 'Mow' vineyards (8.0). However, none of these trends was significant (Figure S2).

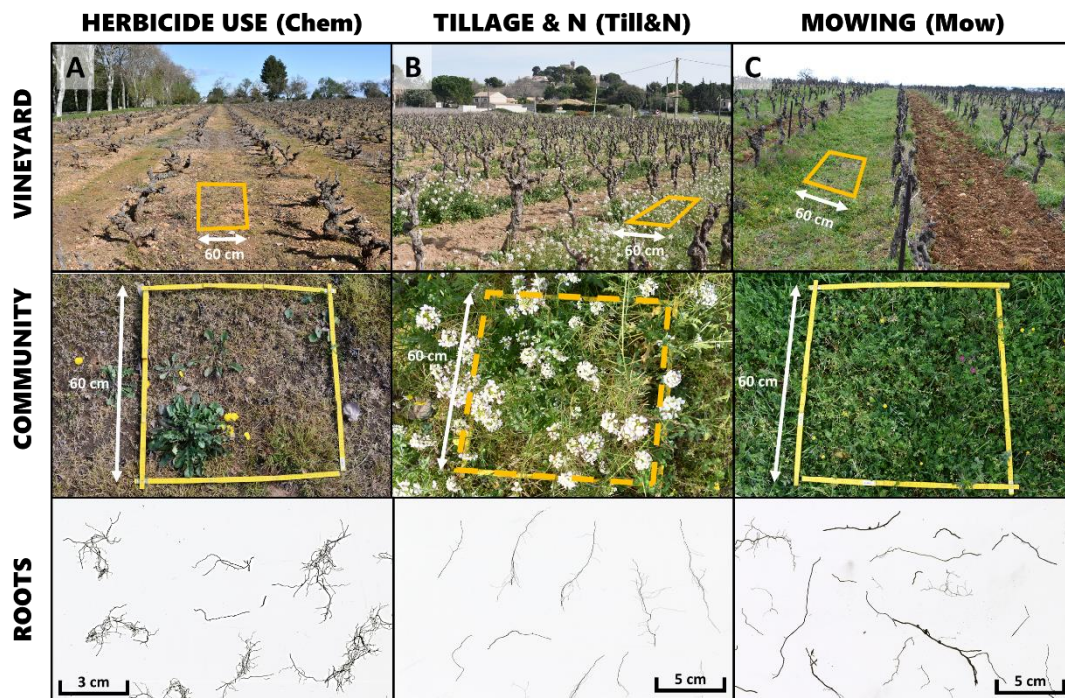


Figure 3 Example of vineyards of the network managed with herbicides (A), tillage & high nitrogen fertilization rates (B) and mowing (C). Top panels show the inter-rows where one weed community was sampled, middle panels are the pictures of the sampled weed community, below panels are the scans of roots that were sampled within the quadrats of weed communities of the middle panels.

### 3. Aboveground functional properties of weed communities measured at the species level and scaled up to the community level

In each vineyard, four quadrats of 60 × 60 cm were randomly placed in neighbouring inter-rows, delimiting four random weed communities per vineyard (Figure 3). In total, 60 weed communities (4 quadrats × 15 vineyards) were characterized for this study. In each quadrat, the plant



species were identified and their covers were quantified to estimate their relative abundances. Across this network of 15 vineyards, 83 species were identified. We sampled the weed communities in March 2020 before the first weed management interventions. We identified the list of the most abundant species for each community that covered at least 80 % of the quadrats to measure their leaf traits.

Four aboveground traits were measured: specific leaf area (SLA), leaf dry matter content (LDMC), leaf carbon to nitrogen ratio (C: N) and height. SLA, LDMC and height were measured following Pérez-Harguindeguy et al.'s (2016) methodology on eight individuals per species collected nearby the quadrats in the inter-rows. Leaf C:N was measured by pooling and grinding all eight individual leaves per species with three repeated measures by elemental analysis (NF ISO 10694) using a FlashSmart 2000NC HPAR analyser (ThermoFisher Scientific, Mylan, Italy). To scale up from species to communities, we calculated the community-weighted means of the leaf traits (CWM) (Garnier et al., 2004) by applying the Mass Ratio Hypothesis which states that the most dominant species of a community drive the ecosystem processes (Grime, 1998):

$$CWM = \sum_{i=1}^n p_i \times trait_i \text{ (Eq. 1)}$$

where  $p_i$  is the relative abundance of the species  $i$  within a community,  $trait_i$  is the value of trait of the species  $i$  and  $n$  is the number of species within the community. Community weighted mean expresses the most probable trait value of an individual plant within a community.

#### **4. Belowground functional properties measured at the community level**

In addition to aboveground traits, four root traits were measured at the community level. Roots were extracted from one soil core (diameter of 8 cm x 10 cm of depth), that was sampled in each quadrat in contrast with the soil core samples for basic description of soil characteristics sampled outside the quadrats. After being stored in a freezer for two months, soil cores were defrosted at room temperature and roots were washed. Fine roots were selected (< 2 mm in diameter) and spread in a clear acrylic tray filled with distilled water to be scanned at 800 dots per inch (Epson Expression 1680; Epson, Ontario, Canada). The scans were processed using digital image analysis software (WinRhizo Pro, v.2009c; Regent Instruments, Quebec, Canada). The total root length per diameter class and volume of each root was determined. After being scanned, root samples were oven-dried at least 48h at 60°C and their dry mass was weighed. Root carbon to

nitrogen ratio (root C:N) was measured following the same methodology as the leaves. Root mean diameter (D), specific root length (SRL ; total root length to root dry mass ratio) and root tissue density (RTD ; root dry mass to root volume ratio) were computed based on the analyses of scans and root dry mass.

## 5. Potential microbial activities

Three soil cores were sampled within each quadrat (diameter of 8 cm x 10 cm of depth), nearby the soil core from which roots were extracted, and were stored in a freezer for two months. Then, soil cores were defrosted at room temperature for one week before sieving them (2mm) and measuring their potential microbial activities. Three potential microbial activities were measured: (i) Substrate-Induced Respiration (SIR), (ii) Nitrifying Enzyme Activity (PNEA) and (iii) Denitrifying Enzyme Activity (PDEA). These indicators proxy the potential activity of different enzymes pool with no limiting factor.

SIR was measured following Beare et al. (1990). Twenty grams of fresh soil were incubated with 1.5 mg C-glucose per gram of dry soil in a 150 ml serum flask and 80% of water-holding capacity. The amount of C-CO<sub>2</sub> produced by the soil samples at 25°C was quantified for 4 hours (from t<sub>0</sub>+2h and t<sub>0</sub>+6h) using a micro-catharometer (MicroGC, SRA, Marcy l'Étoile, France). SIR was computed as the amount of C-CO<sub>2</sub> produced per gram of dry soil per hour.

PDEA was measured following Smith and Tiedje (1979). Twenty grams of fresh soil were inserted into a 150-ml serum flask in anoxic conditions with 10% acetylene to inhibit the transformation of N<sub>2</sub>O to N<sub>2</sub>. Sources of carbon and nitrogen were added at t<sub>0</sub>: glucose, glutamic and nitrate at 1, 1 and 0.1 mg C or N per gram of dry soil, respectively. DEA was computed from the amount of N<sub>2</sub>O produced in 4 hours (from t<sub>0</sub>+2h and t<sub>0</sub>+6h) at 25°C quantified with a CP-3800 gas chromatographer equipped with an electron capture detector (Varian, Palo Alto, USA).

PNEA was measured following Lensi et al. (1986). Twenty grams of fresh soil were inserted in two 150-ml serum flasks: one to estimate the amount of nitrate that was already in the soil (F1) and the second one to estimate the amount of initial nitrate and the amount of inserted ammonium than can be converted in nitrate in optimal conditions (F2). In F1, we inserted 1 mg C.g<sup>-1</sup> dry soil (glucose and glutamic acid) and a suspension of active denitrifying bacterial strain (*Pseudomonas fluorescens AK15*) prepared at a final concentration of optical

density at 580 nm = 2.0 for a 5 ml suspension per flask. In anoxic conditions, we added 10% acetylene into the flasks to inhibit the transformation of  $N_2O$  to  $N_2$ . The F1 flasks were kept at 25°C with water content at 100% of the water-holding capacity for 24 h (the time it takes for the total amount of nitrate to be converted to nitrous oxide). F2 flasks were incubated in oxic conditions for 48h with 0.2 mg of  $N-(NH_4)_2SO_4$  g<sup>-1</sup> dry soil at 80% of the water-holding for nitrification to occur. Then, F2 flasks were incubated in the same conditions as F1 for denitrification to occur.  $N_2O$  was quantified the same way as for PDEA. The difference between  $N_2O$  produced in F2 (inserted ammonium converted to nitrate + initial nitrate) and F1 (initial nitrate) estimated PNEA.

Three microbial variables were used or calculated to characterise the functional properties of microbial communities related to the recycling of nitrogen. First, SIR was selected as a proxy for heterotroph microbial biomass. Second, the ratios of PDEA:SIR and PNEA:SIR were calculated to estimate the abundance of denitrifiers and nitrifiers relative to the soil heterotroph microbial communities (Schimann et al., 2012). In the rest of this study, we simplify the meaning of these ratios as “relative abundance”.

## 6. Data analyses

Two datasets were used in the present study: the community-level dataset (n=60 communities with vineyard as random effect) and the vineyard-level dataset (n=15 averaged community per vineyard). To characterise the covariations between aboveground and belowground traits at the community level, we computed a PCA based on the community-level dataset (n=60 communities). We tested if weed communities managed by different practices had different coordinates on the first three axes and for each functional parameter (CWM and root traits). We performed ANOVA on these models (type III). To test if microbial functional properties (SIR, PNEA:SIR, PDEA:SIR) were related to weed functional variables, we performed mixed linear models using the community-level dataset (n=60 communities). In each model, we added weed functional property metrics as fixed effects (CWM, community level root traits, coordinates of communities along the first three axes of the functional PCA and root biomass) and vineyard as random effect. As aboveground biomass and root biomass were positively correlated ( $\rho = 0.34$ ,  $P = 0.01$ ), we chose to only keep root biomass in the models.

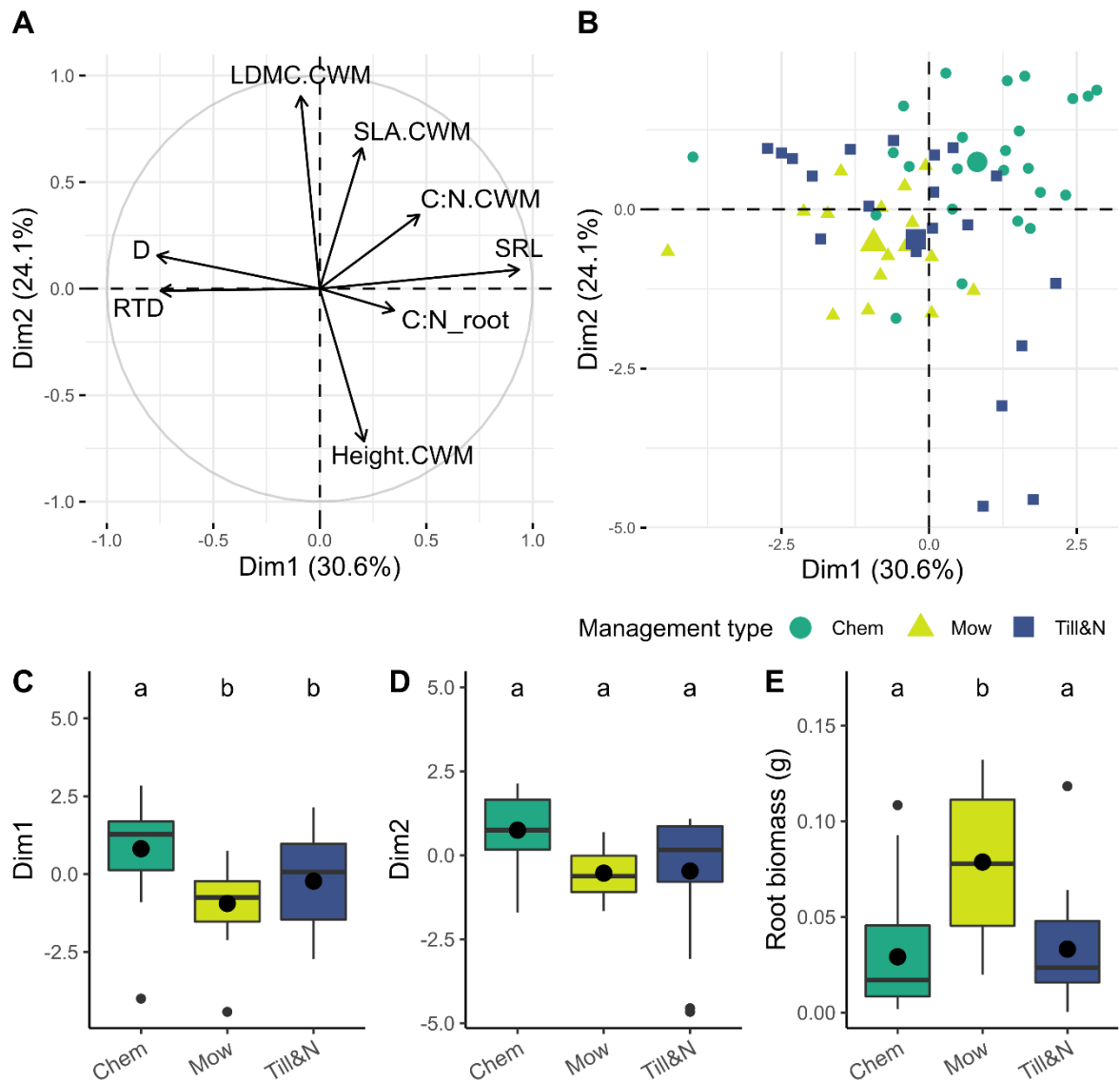
To explore the effect of management, soil, climate and weed functional properties that were significantly related to the microbial functional properties (SIR, PNEA:SIR, PDEA:SIR), we performed linear models using the vineyard level dataset (n=15 vineyards). For each model presented in this paper, we checked that the variation inflation factor was lower than five. Then, we used model averaging to select the best explaining model using the corrected Akaike information criterion (AICc). All data analyses were carried out using R version 4.1.1 (R Core Team, 2021).

# RESULTS

## 1. Above and belowground response traits of weed communities to management

Aboveground dry biomass of mowed weed communities (55 g on average per 60x60 cm<sup>2</sup> quadrats) was higher than chemically weeded communities (21 g) (Figure S3). The cover rates of mowed communities (91%) were also higher compared to tilled and chemically weeded communities (59% for both) (Figure S3). Mowed communities were composed of more species (14 species on average) than tilled and chemically weeded communities (7 and 5 species respectively) (Figure S3). Legume species were more abundant in mowed communities (36% of cover rate) compared to the other communities (29% in tilled communities and absent from the chemical controlled communities).

The first two axes of the functional PCA exploring aboveground and root trait covariations explained 55% of the functional variability across communities (Figure 4A). The first axis that explained most of the functional variation (31%) was driven by community-level root traits. This axis opposed weed communities with high SRL to communities with high root diameters and high RTD. SRL covaried negatively with root diameter ( $-0.72$ ,  $P < 0.001$ ) and RTD ( $-0.71$ ,  $P < 0.001$ ) (Table S2). The second axis was explained by aboveground CWM (24% of explained variation). This axis discriminated weed communities dominated by species with high LDMC and high SLA to high-stature communities. SLA and LDMC were positively correlated ( $0.63$ ,  $P < 0.001$ ) (Table S2). The third axis was driven by SLA, height, root C:N and leaf C:N to a lesser extent and explained 16% of the functional variance (Figure S4). This axis opposed high-stature weed communities with high SLA and high root C:N to smaller communities with low SLA and root C:N (Figure S4). Some aboveground and belowground functional community level metrics also covaried significantly: leaf C:N was positively correlated with root C:N ( $0.44$ ,  $P = 0.02$ ) and SRL ( $0.44$ ,  $P = 0.01$ ) (Table S2).



**Figure 4** **A** Circle of correlation of the aboveground community weighted means (CWM) and community-level root traits. **B** Weed communities displayed on the first two axes of the functional PCA. Each dot is a weed community whose colour and form refer to weed management of the corresponding vineyards. **C** Weed community coordinates along the first axis of the functional PCA according to weed management. **D** Weed community coordinates along the second axis of the functional PCA according to weed management. **E** Root biomass according to weed management. Different letters indicate a significant difference (Student's *t*-test with  $\alpha = 0.05$ ). LDMC.CWM, leaf dry matter content ; SLA.CWM, specific leaf area ; C:N.CWM, leaf carbon to nitrogen ratio ; SRL, Specific Root Length ; C:N\_root, carbon to nitrogen ratio of the roots ; RTD, Root Tissue Density ; D, root diameter ; Chem, 5 years of chemical weeding ; Mow, 5 years of mowing and long period of weed cover presence and amendment ; Till&N, 5 years of tillage on the inter-rows and chemical weeding on the rows with high fertilisation input.

Weed communities managed with herbicides had contrasting root trait values along the first axis of the functional PCA driven by root traits (SRL, root diameter, RTD) compared to the communities managed with tillage or mowing (Figure 4B, C). Weed management significantly impacted SRL while RTD and root diameter did not respond significantly (Figure 5), demonstrating that it was mostly SRL that drove the differences in coordinates of weed communities along the first PCA axis. Weed communities controlled by chemical weeding had significantly higher SRL (mean  $282 \pm \text{sd } 112 \text{ m.g}^{-1}$ ) than tillage (mean  $196 \pm 89 \text{ m.g}^{-1}$ ) and mowing ( $157 \pm 67 \text{ m.g}^{-1}$ ) (Figure 4C, Figure 5 ; Table S3). Management did not significantly impact the coordinates of weed communities along the second axis of the functional PCA driven by aboveground traits (SLA, LDMC, height) and the third axis driven by SLA, height and root C:N neither (Figure 4B, D ; Figure S4). Weed communities that were located in vineyards controlled by chemical weeding had higher community weighted leaf C:N ( $17.4 \pm 2.8$ ) than tilled ( $13.2 \pm 2.6$ ) and mowed communities ( $13.5 \pm 1.8$ ) while root C:N were not significantly different across weed management (Figure 5 ; Table S3). The root biomass of weed communities was higher in mowed vineyards ( $77 \pm 37 \text{ mg}$ ) than in tilled ( $33 \pm 28 \text{ mg}$ ) and chemically weeded vineyards ( $29 \pm 30 \text{ mg}$ ) (Figure 4B, E).

## **2. Relationship between the above and belowground traits of weed communities and N-cycling properties of the microbial communities**

Weed communities with high SRL were associated with vineyard soils with high PNEA:SIR (estimate: 0.48,  $P = 0.016$ , Table 1). RTD was also selected in the best-averaged model but its estimate was not significant. Soil microbial biomass (SIR) and the relative abundance of denitrifiers (PDEA:SIR) were not explained significantly by the aboveground CWM, the root traits and the root biomass. Most of the SIR and PDEA:SIR variances were explained by the random effect 'vineyard' (87% for PDEA:SIR and 78% for SIR), suggesting that pedoclimate and management might strongly impact these variables. The first three dimensions of the functional PCA based on aboveground and belowground traits (Figure 4) did not explain significantly SIR, PNEA:SIR and PDEA (Table S4)

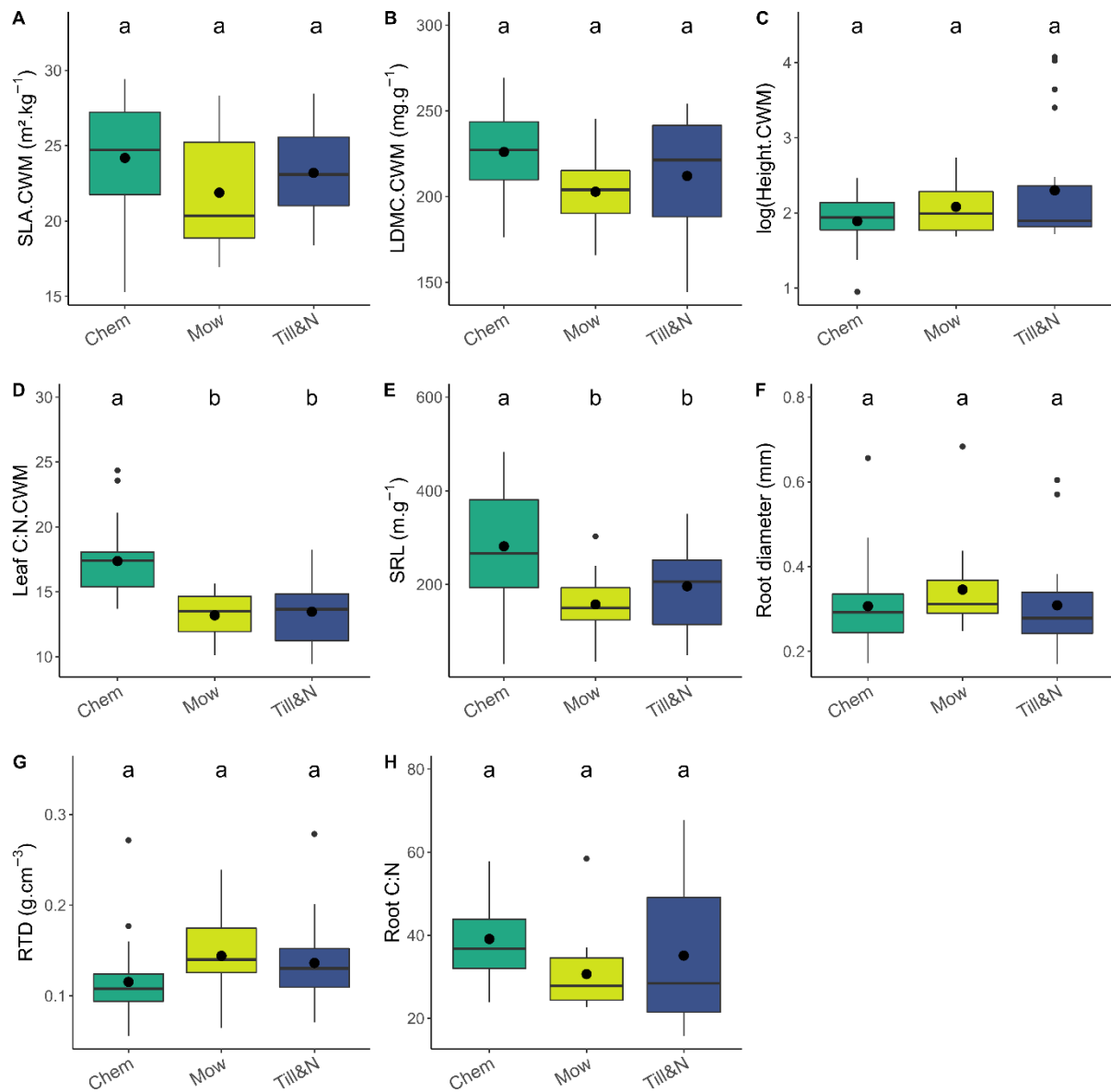


Figure 5 Aboveground community weighted means (CWM) and root traits at the community level according to the management practices. Different letters indicate a significant difference (Student's *t*-test with  $\alpha = 0.05$ ). SLA, Specific Leaf Area ; LDMC, Leaf Dry Matter content ; Leaf C:N, leaf carbon to nitrogen ratio ; SRL, Specific Root Length ; RTD, Root Tissue Density ; Root C:N, root carbon to nitrogen ratio ; Chem, communities controlled by chemical weeding for five years ; Mow, communities controlled by mowing for five years with vinasse inputs ; Till&N, communities controlled by tillage for five years with high fertilisation inputs.



Table 1 Standardised estimates of the weed functional properties (aboveground community weighted means, CWM ; community-level root traits and root biomass) explaining N-related microbial functional properties (SIR, PNEA:SIR, PDEA:SIR) (n=60). Significant p-values ( $p < 0.05$ ) are in bold. The full model was composed of above-ground CWM (SLA, LDMC, height, leaf C:N), root traits (SRL, root diameter, RTD, root C:N) and root biomass as fixed effects and a ‘vineyard’ random effect. Std. est., standardised beta estimates; Std. err., standardised errors; t, t-value; P, p-value;  $R^2_{\text{marg}}$ , marginal  $R^2$ ;  $R^2_{\text{conds}}$ , conditional  $R^2$ ;  $AICc_{\text{full}}$ , corrected Akaike information criterion of the full model ;  $AICc_{\text{sel}}$ , AICc of the selected model ; SIR, Substrate Induced Respiration ; PNEA, Potential Nitrifying Enzyme Activity ; PDEA, Potential Denitrifying Enzyme Activity ; SRL, Specific Root Length ; RTD, Root Tissue Density.

Explained variables	Explaining variables	Std. est.	Std. err.	t	P	$R^2_{\text{marg}}$	$R^2_{\text{cond}}$	$AICc_{\text{full}}$	$AICc_{\text{sel}}$
Microbial biomass (SIR)	Root biomass	-0.04	0.03	-1.19	0.241	1%	87 %	106.6	54.9
Relative abundance of nitrifiers (PNEA:SIR)	SRL	0.48	0.19	2.50	<b>0.016</b>	12%	39 %	-91.6	-319.9
	RTD	0.34	0.18	1.93	0.060				
Relative abundance of denitrifiers (PDEA:SIR)	-	-	-	-	-	0%	78 %	147.3	103.4

### 3. Effects of management, soil abiotic characteristics, climate and functional properties of weed communities on the functional properties of microbial communities related to N cycling

Microbial biomass (SIR), the relative abundance of nitrifiers (PNEA:SIR) and denitrifiers (PDEA:SIR) did not covary significantly (Table S5). Among all the variables tested (pedoclimate, weed management, weed functional properties), only soil abiotic characteristics (pH and %Sand) and weed management were selected in models explaining variation in soil microbial biomass (SIR) (Table 2). Acidic soils with low sand content had high microbial biomass. Mowed vineyards had higher soil microbial biomass ( $17.2 \pm 9.5 \mu\text{g C-CO}_2\text{.g}^{-1}\text{.h}^{-1}$  on average) compared to vineyards using tillage ( $7.1 \pm 2.8 \mu\text{g C-CO}_2\text{.g}^{-1}\text{.h}^{-1}$ ) (Figure 6). Vineyards managed with herbicides did not have a significant difference in soil microbial biomass compared to tillage and mowing ( $8.3 \pm 4.6 \mu\text{g C-CO}_2\text{.g}^{-1}\text{.h}^{-1}$  on average) (Figure 6).

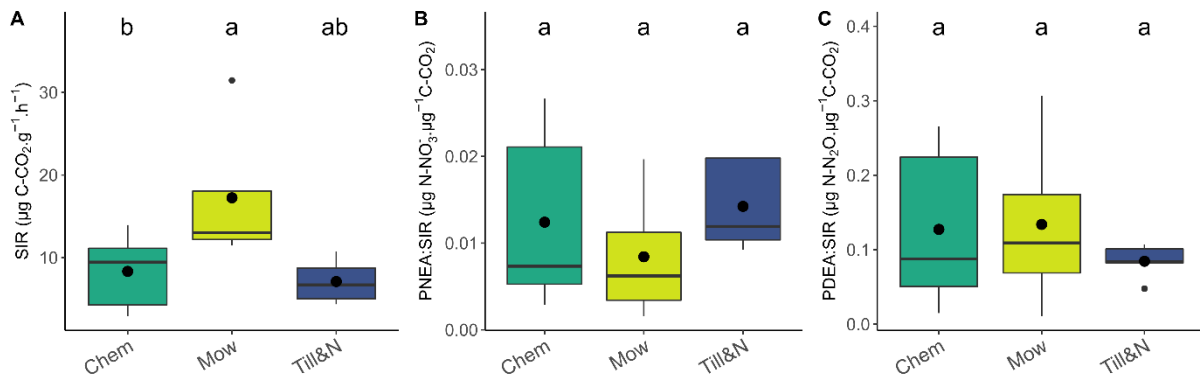


Figure 6 Microbial community properties of vineyard soils according to weed management. SIR, substrate-induced respiration (microbial biomass) ; PNEA:SIR, potential nitrifying enzyme activity to substrate-induced respiration ratio (nitrifier relative abundance) ; PDEA:SIR, potential denitrifying enzyme activity to substrate-induced respiration ratio (denitrifier relative abundance). Different letters indicate a significant difference of potential microbial activities.

The relative abundance of nitrifiers in microbial communities (PNEA:SIR) was only explained by SRL of associated weed communities (no climate, soil or management variables were selected) (Table 2). Communities with do-it-yourself strategies (high SRL) were associated with

microbial communities with a high relative abundance of nitrifiers (estimate: 0.53,  $P = 0.041$ ). If the significance of the effect was quite low ( $P = 0.041$ ), the standardised coefficient of the effect of SRL was quite high (0.53) (Table 2).

The relative abundance of denitrifiers in microbial communities (PDEA:SIR) was explained by the same soil variables (pH and %Sand) as microbial biomass while management and climate variables were not selected in the final models (Table 2). Alkaline soils with low sand content had a higher abundance of denitrifiers within microbial communities.

*Table 2 Standardised estimates of climate, soil, management and weed functional properties explaining the microbial functional properties (n=15). Significant p-values ( $p < 0.05$ ) are in bold. The full model of SIR and PDEA:SIR were constituted of one climate variable (aridity index), three soil variables (pH, %Sand, soil organic matter) and weed management as fixed effects. The full model of PNEA:SIR was constituted of the same variables as the other models with the specific root length (SRL) as additional fixed effect. Std. est., standardised beta estimates; Std. err., standardised errors; t, t-value; P, p-value;  $R^2$ , adjusted  $R^2$ ;  $AICc_{full}$ , corrected Akaike information criterion of the full model;  $AICc_{sel}$ , AIC of the selected model; SIR, Substrate Induced Respiration; PNEA, Potential Nitrifying Enzyme Activity; PDEA, Potential Denitrifying Enzyme Activity.*

<b>Explained variables</b>	<b>Explaining variables</b>	<b>Std. est.</b>	<b>Std. err.</b>	<b>t</b>	<b>P</b>	<b><math>R^2</math></b>	<b><math>AICc_{full}</math></b>	<b><math>AICc_{sel}</math></b>
Microbial biomass (logarithmised SIR)	pH	-0.28	0.07	-4.07	<b>0.001</b>	74%	48.8	37.3
	%Sand	-0.27	0.07	-3.13	<b>0.002</b>			
	Weed management 'Mow' compared to 'Chem'	0.36	0.16	2.36	<b>0.040</b>			
	Weed management 'Till&N compared to 'Chem'	0.12	0.14	0.31	0.762			
Nitrifier relative abundance (PNEA:SIR)	SRL	0.53	0.23	2.27	<b>0.041</b>	8%	-58.8	-99.4
Denitrifier relative abundance (PDEA:SIR)	pH	0.24	0.08	4.95	<b>&lt;0.001</b>	68%	56.1	32.4
	%Sand	-0.21	0.08	-2.57	<b>0.024</b>			

# DISCUSSION

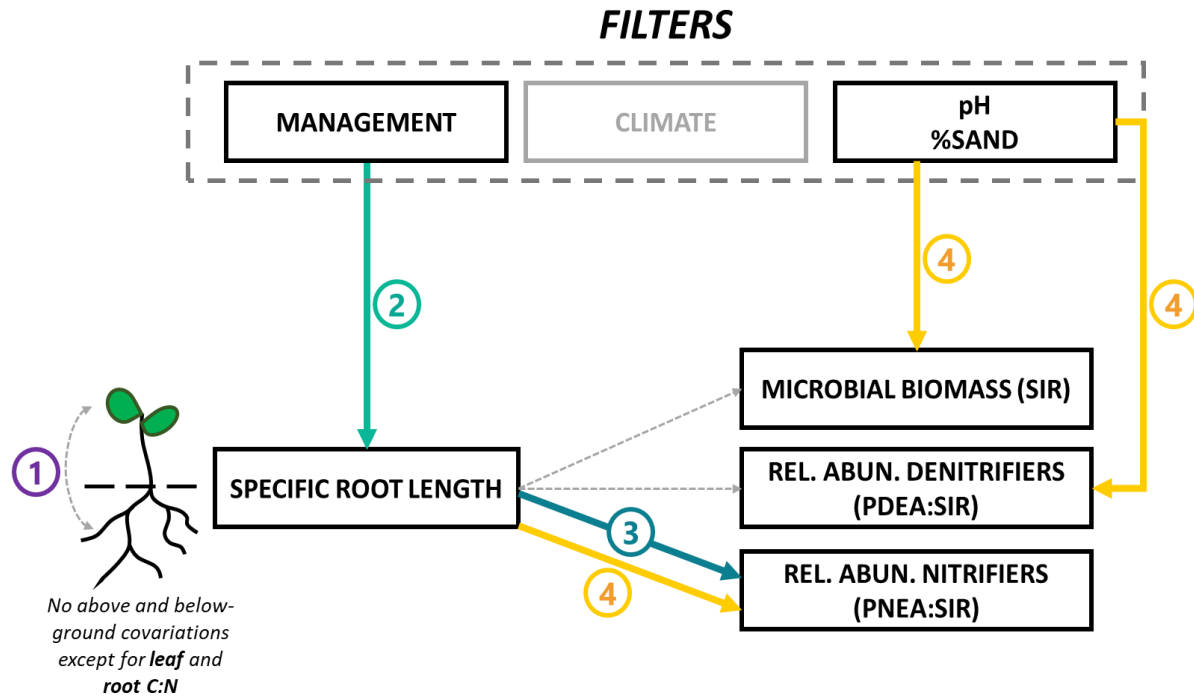


Figure 7 Main results of the study. First, we showed that aboveground and belowground functional properties of weed communities varied independently (arrow 1), except for leaf and root C:N that covaried positively. Second, we demonstrated that management was the main driver of specific root length at the community level (arrow 2) while soil abiotic characteristics had little effect and climate no effect on the functional properties of weed communities. Third, we showed that specific root length was positively correlated with the relative abundance of nitrifiers (PNEA:SIR) (arrow 3) while no functional property of weed communities correlated significantly with microbial biomass (SIR) or to the relative abundance of denitrifiers (PDEA:SIR). Fourth, we found that microbial biomass (SIR) and the relative abundance of denitrifiers (PDEA:SIR) were explained by pH and the percentage of sand in the soils while the relative abundance of nitrifiers PNEA:SIR was explained by the specific root length of weed communities (arrows 4). Bold arrows depict significant correlations and dotted arrows signify no correlation.

Three key findings were obtained in this study (Figure 7). First, management significantly affected weed belowground strategies: herbicide uses for five years filtered weed communities with more do-it-yourself strategies while tillage and mowing selected for more collaborative weed communities (30% lower SRL for tilled communities and 44% lower SRL for mowed communities compared to weed communities managed with chemical control). Second, the relative abundance of nitrifiers (PNEA:SIR) was driven by the SRL of the weed communities (pedoclimate and management factors

were not selected in the models). Third, in contrast, abiotic soil characteristics (pH and sandy texture) were the main drivers of the microbial biomass (SIR) and the relative abundance of denitrifiers within soil microbial communities (PDEA:SIR). To a lesser extent than soil abiotic characteristics, management also impacted microbial biomass (SIR): mowed weed communities had 58% higher SIR compared to chemically weeded communities.

### **1. Covariation of aboveground and belowground traits of weed communities in a gradient of management in Mediterranean vineyards**

From a functional PCA based on an equal number of above and belowground traits, we found that root traits of weed communities explained more variation than aboveground traits. The first axis of the functional PCA represented the fungal collaboration gradient. This gradient ranges from collaborative and outsourcing weed communities with high root diameters to do-it-yourself communities with high SRL and carbon-efficient root (Bergmann et al., 2020). This gradient was found at the species level (Bergmann et al., 2020) and the community level along land-use gradients and ecological successions (Erktan et al., 2018; Prieto et al., 2015). This SRL-root diameter pattern, emerging across the different levels of organisation and in both natural and managed ecosystems suggests that similar constraints operate across scales and land uses. However, species-level studies demonstrated that RTD and the collaborative gradient (SRL-root diameter) were decoupled and that RTD covaried negatively with root nitrogen content (Bergmann et al., 2020; Carmona et al., 2021; Weigelt et al., 2021). In our study, we found that RTD covaried negatively with SRL at the community level and was not correlated to root C:N. This could be explained by the major plant growth form composing weed communities: herbaceous species. At the species level, Wang et al. (2017) and An et al. (2022) also found a negative correlation between SRL and RTD when considering only herbaceous species while these two traits were uncoupled for woody species. These differences in phenotypic integration in woody and non-woody species were explained by the different distribution of functions within the root systems (Roumet et al., 2016). In woody species, the first-order roots' function is resource acquisition while higher order roots' functions are anchorage and resource transport. In herbaceous species, first-order roots are multifunctional, ensuring resource acquisition

as well as support and transport functions. This root multifunctionality might couple root trait values driving different functions achieved by the same root unit (*e.g.* soil resource exploration for SRL or root mechanical resistance for RTD).

In the weed communities of this study, morphological aboveground (SLA, LDMC, height) and belowground traits (SRL, root diameter, RTD) were decoupled. This independence of aboveground and root traits can occur for several reasons at the community level. First, root traits were measured at the community level using the pooled-species approach (Wang et al., 2021) while aboveground traits were measured at the species level and then scaled up using community-weighted means. These different ways of estimating aboveground and belowground properties might partially explain the community functional uncoupling of these morphological traits. Second, leaf and root traits are not functional analogues (Weemstra et al., 2016). Leaves' function is maximising light and CO<sub>2</sub> capture while reducing resource loss due to herbivory (Poorter et al., 2009). In contrast, root's first functions are water capture and essential mineral absorption (Weemstra et al., 2016). Third, aboveground and belowground traits do not face the same constraints and might be independently filtered in different environments (Erktan et al., 2018). Soil texture, structure and chemistry represent strong constraints for root functionality (*i.e.* for instance, physical constraints due to compacted soil structure) that do not impede aboveground traits (Weemstra et al., 2016). In the case of vineyards, weed management can also create differential filtering on aboveground and belowground biomass. For instance, mowing destroys mostly the aboveground biomass while belowground biomass is barely affected. Compared to unmowed environments, Erktan et al. (2018) showed that mowing decorrelated some aboveground and belowground traits at the community level (LDMC and root dry matter content) due to reduced investment in aboveground traits while the investment in belowground remained unchanged.

In contrast with aboveground and belowground morphological traits, C:N of leaves and roots covaried positively. Several studies also found this positive covariation between C:N of above and belowground organs at the community level (Erktan et al., 2018; Prieto et al., 2015; Wang et al., 2017). High nitrogen content in roots is a good proxy of the capacity of resource acquirement and tissue metabolic activity, which is associated with increased photosynthetic export and phloem

loading. Thus, whole species-level allocation rules seem to drive the partitioning of nutrients to above and belowground organs, translated at the community level.

## **2. Community-level root trait response to management in weed communities in Mediterranean vineyards**

Management significantly leaf C:N ratio and impacted SRL of weed communities. Leaf C:N describes the investment in carbon in tough and resistant leaf structures with regards to the investment in photosynthetic enzymes. Five years of chemical weeding selected weed communities with resistant and long-lived leaves (23% higher leaf C:N ratio than tilled and mowed communities) and do-it-yourself strategies (30% and 44% higher SRL compared to tilled communities and mowed communities, respectively). In contrast to our hypotheses, herbicides selected resource-conservative aboveground strategies while chemical weeding is usually conceptualised as a disturbance that would favour acquisitive strategies (Gaba et al., 2014). However, chemical weeding might also be considered as a stress for several reasons. First, Lichtenthaler (1998) states that “stress is a dose-dependent matter”. The effectiveness of herbicides is indeed related to a registered dose. If the dose is too low, herbicides can have opposite effects and stimulate plant growth (Lichtenthaler, 1998). Second, herbicides are selective and some glyphosate-tolerant species (*e.g. Malva sylvestris*) or resistant (*e.g. populations of Lolium perenne*) might survive while disturbance destroys all biomass indiscriminately. Moreover, a high leaf C:N might be due to the presence of a thick cuticle or high wax content of leaves that decreased glyphosate absorption (Santier and Chamel, 1992). Glyphosate, which was the main active ingredient of the herbicides used by the farmers of the study network, has been shown to strongly decrease root colonisation by arbuscular mycorrhizal fungi (AMF) and the viability of the spores, even at low doses (Druille et al., 2013). The targeted enzyme of glyphosate (5-enolpyruvylshikimate-3-phosphate ; EPSP) does not only exist in plants but also in bacteria and fungi (Padgett et al., 1995), thus causing a detrimental effect on their survival. Colonisation by AMF was found to correlate positively with root diameter (Bergmann et al., 2020). High SRL species tend to collaborate less with mycorrhizal fungi (Bergmann et al., 2020). Thus, the application of glyphosate might have filtered out species with high AMF colonisation and low specific root length.

### **3. Nitrifier, denitrifiers relative abundance and microbial biomass in response to management and relation with root traits**

Substrate-induced respiration and the relative abundance of nitrifiers and denitrifiers varied strongly over the different weed communities (respective coefficient of variation of 93%, 123% and 71%). SIR was quite similar to the values measured in grasslands (Orwin et al., 2018), in annual crops (Mijangos et al., 2006; Simonin et al., 2018) and in vineyards (Simonin et al., 2018). PNEA ranged from close to 0 to  $0.42 \mu\text{g N-NO}_3^- \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  (mean  $0.11 \mu\text{g N-NO}_3^- \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) (Table S6) and was narrower than the range of values measured in annual crop systems (Simonin et al., 2018) and to a lesser extent, in vineyards (Simonin et al., 2018). DEA ranged from 0.08 to  $6.69 \mu\text{g N-N}_2\text{O} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  (Table S6) and was quite high compared to subalpine grasslands (Cantarel et al., 2015; Robson et al., 2007), annual crops systems (Simonin et al., 2018) and vineyards (Simonin et al., 2018). This is quite surprising if we consider the unfavourable conditions for denitrification to occur in Mediterranean vineyards (low soil water content, low fertilisation and nitrate availability). If potential microbial activities might not represent the real microbial activities in the vineyards, they allow to control *in-situ* enzyme activity fluctuations due to daily changing conditions (temperature, water content) and to easily compare vineyard soil abundance of nitrifiers and denitrifiers from different vineyards (Fromin et al., 2010).

Do-it-yourself weed communities (high SRL) were associated with a higher relative abundance of nitrifiers. As SRL was negatively correlated with root diameter and root tissue density in our study, we also indirectly showed that collaborative and conservative weed communities were associated with low relative abundance of nitrifiers within the microbial communities. Resource-acquisitive species (high SRL, low root diameter, low RTD) are characterised by a high N uptake (Abalos et al., 2019), high root turnover (Freschet et al., 2020) and a high carbon rhizodeposition (Henneron et al., 2020). This strategy has been hypothesized and shown to induce faster soil N cycling (Henneron et al., 2020). The release of easily degradable carbon rhizodeposits might enhance soil microbial activity and nitrogen mineralisation, increasing soil ammonia concentration available for nitrification. This faster N cycling and thus faster nitrification might explain the higher relative



abundance of nitrifiers associated with weed communities characterised by high SRL. Moreover, weed communities with high SRL might absorb more water and thus favour oxic soil conditions, necessary for the nitrification process. However, the shallow sampling (10 cm deep) and the dry conditions of soils due to Mediterranean irregular rainfall make this explanation less plausible. At the species level, with seven perennial grass and one dicotyledonous species grown in pots, Cantarel et al. (2015) found that NEA was negatively related to SRL. This contrasting result might be due to the scaling up from species to the community level and abundance weighting, to the domination of annual weed species in the communities of our study, which occupied a different place in the root economics spectrum than perennials (Roumet et al., 2016) or due to environmental constraints that exist in vineyards and not in controlled pot experiments.

SIR and the relative abundance of denitrifiers were mostly explained by pH and the percentage of sand in the soils. Alkaline soils with low sand content had a higher relative abundance of denitrifiers within microbial communities. Denitrification potential was found to be negatively related with the percentage of sand in the soils due to better drainage and lower water holding capacity that decrease anoxic conditions (Matson and Vitousek, 1987). Moreover, denitrification is higher in neutral or alkaline soils than in acidic soils, which might be due to the indirect effect of nitrification that is inhibited in acidic soils (Šimek and Cooper, 2002). Acidic soils with low sand content had high microbial biomass. Indeed, fine-textured soils with poor sand content have more numerous and smaller pores that physically protect microbial biomass (Hassink et al., 1993).

Our study showed that the simultaneously measured weed traits and potential microbial activities are poorly related in Mediterranean vineyards. Our synchronic approach was based on the hypothesis that trait values of weed communities measured at a given time are integrative of their 'recruitment' effect on soil microbial communities. However, aboveground and belowground traits vary over plant development from weed germination to vegetative phase (Havrilla et al., 2021). Integrating a time dimension through different measurements over the seasons might help to better understand how time scale influences weed-microbe interactions. Indeed, microbial activities and trait values can be considered as 'fast' indicators like potential microbial activities and weed traits,

that are strongly shape by other agroecosystem variables in contrast to ‘slower’ and more controlling indicators like soil organic matter or soil texture (Walker et al., 2012).

#### **4. Management implications**

There is an urgent need to limit the use of input in agroecosystems, like herbicides. Our study shows that tillage and mowing are good alternatives to chemical weed control, especially mowing. Mowed communities produced the highest aboveground and belowground biomass and were characterised by the highest species richness compared to the other management. They were composed of more N-fixing species. Mowed communities had collaborative belowground strategies and acquisitive aboveground strategies. Mowing favoured higher microbial biomass in our study but had no significant effect on nitrifiers and denitrifiers communities. Using almost the same network of vineyards, Bopp et al. (2022) demonstrated that mowed communities were also more decomposable than chemically controlled communities and had a higher nitrogen content within the aboveground biomass. Thus, mowing might represent both a mean to control weed competition but also an amendment practice, restituting high biomass with high nitrogen content and decomposition potential mulch, favouring high soil microbial biomass. In a more economic perspective, mowing save more fuel than tillage (26% of reduction) but is a more time-consuming practice to implement for winegrowers (Sanford and Go, 2022). Thus, mowing is more expensive than chemical weeding and tillage (Pergher et al., 2020) and financial aids are needed to support winegrowers in their transitions (Gage and Schwartz-Lazaro, 2019).

## **CONCLUSION**

In our study, we demonstrated that management significantly affected aboveground and belowground weed functional properties, but had limited direct effect on the microbial biomass (SIR), the abundance of nitrifiers (PNEA:SIR) and denitrifiers (PDEA:SIR) relative to microbial biomass. pH and soil texture were the main drivers of the relative abundance of denitrifiers and

microbial biomass while nitrifiers were determined by SRL of weed communities. We argue that trait-based approaches in combination with soil analyses can provide a more mechanistic understanding of N cycling in agroecosystems. Our study showed that mowing represents a good alternative to chemical weeding, favouring high soil microbial biomass, that could take advantage of soil processes underlying key agrosystem services.

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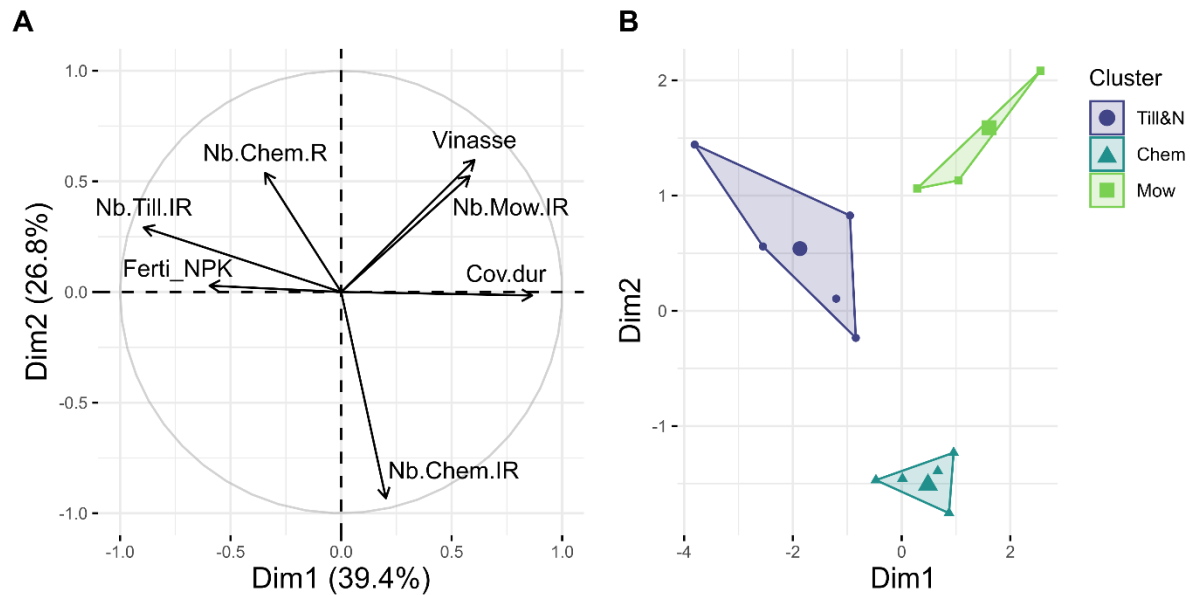
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## SUPPORTING FIGURES



*Figure S1A* Circle of correlation of management variables on the first two axes of the Principal Component Analysis (PCA). All the management variables are averaged over the 2015-2020 period. Nb.Chem.R, number of chemical weeding of the vine rows per year ; Vinasse, annual inputs of vinasse (i.e. residuum after wort distillation) ; Nb.Mow.IR, number of mowing of the inter-rows ; Cov.dur, the annual longest period of weed presence between two destructions by tillage or chemical weeding; Nb.Chem.IR, number of chemical weeding of the inter-rows per year ; Ferti\_NPK, NPK annual inputs ; Nb.Till.IR, number of tillage of the inter-rows. **B** Clustering of vineyards according to their positions in the first two dimensions of the PCA based on the management variables. The dark blue area clusters the five vineyards where the inter-rows are mainly managed by tillage and where the rows are controlled by chemical weeding, with higher fertilisation than the other vineyards of the network. The light blue area groups the six vineyards that are controlled by chemical weeding. The green area clusters the four vineyards that are mowed with a long period of weed cover presence and with inputs of vinasse.



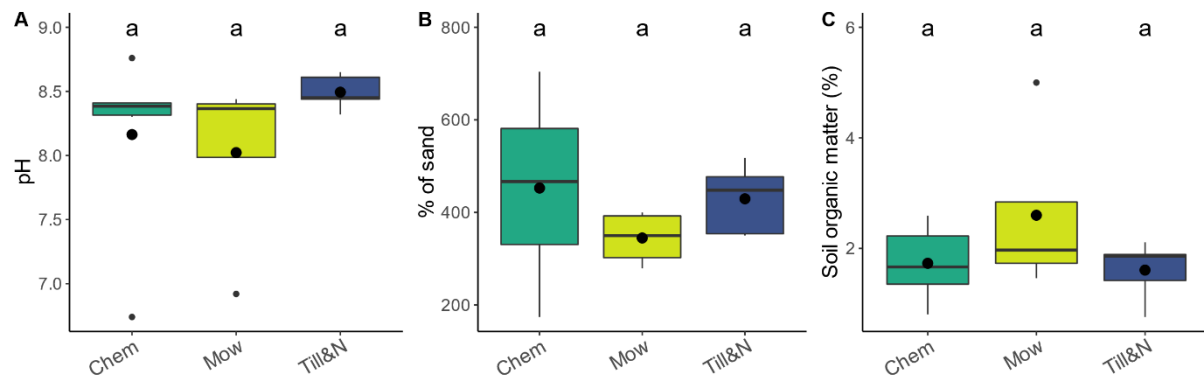


Figure S2 Soil characteristics of vineyards per management type. Different letters indicate a significant difference (Student's *t*-test with  $\alpha = 0.05$ ). Chem, 5 years of chemical weeding ; Mow, 5 years of mowing and long period of weed cover presence ; Till&N, 5 years of tillage on the inter-rows and chemical weeding on the rows with high fertilisation input.

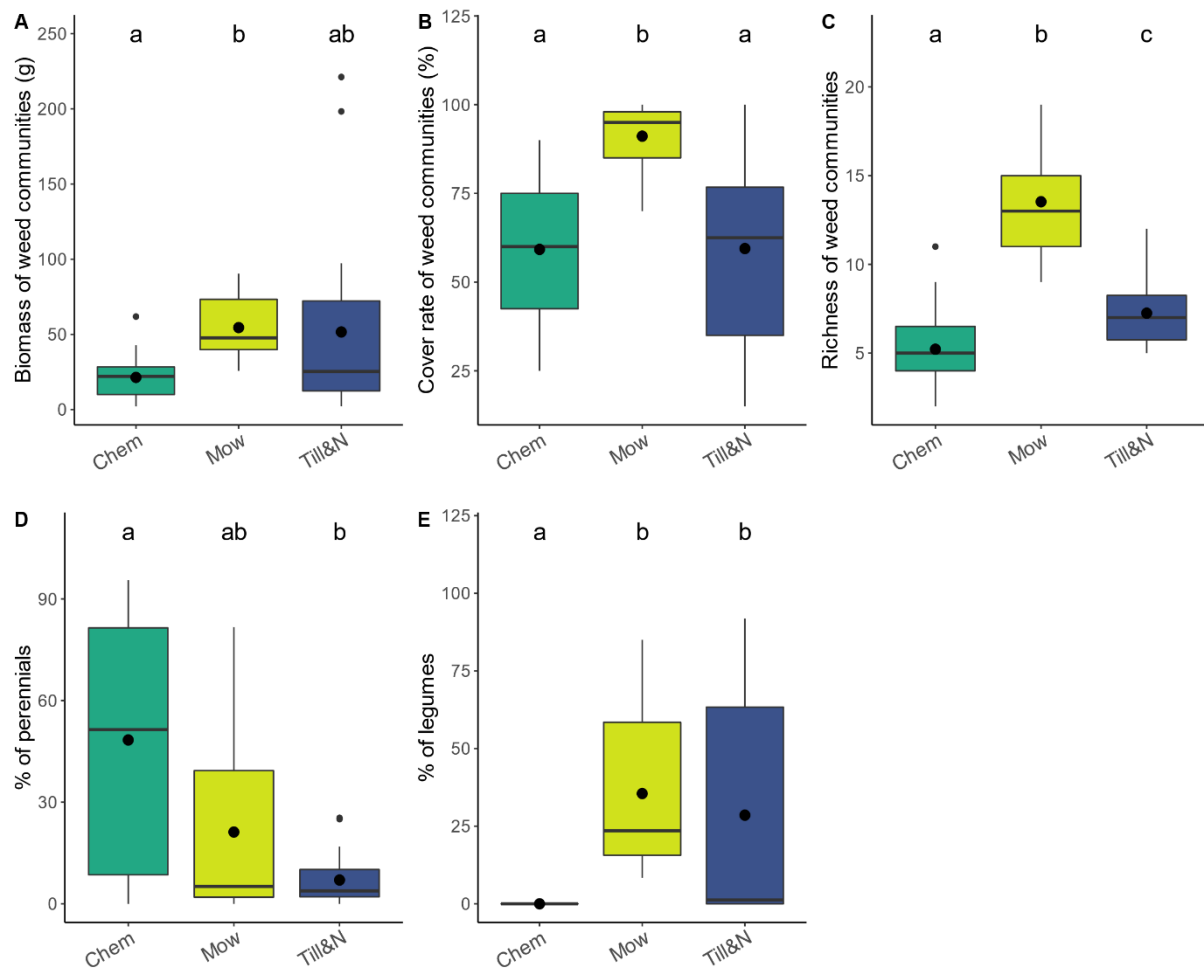


Figure S3 Biomass, cover rate, richness and composition of weed communities. Different letters indicate a significant difference (Student's *t*-test with  $\alpha = 0.05$ ). Chem, 5 years of chemical weeding ; Mow, 5 years of mowing and long period of weed cover presence ; Till&N, 5 years of tillage on the inter-rows and chemical weeding on the rows with high fertilisation input.

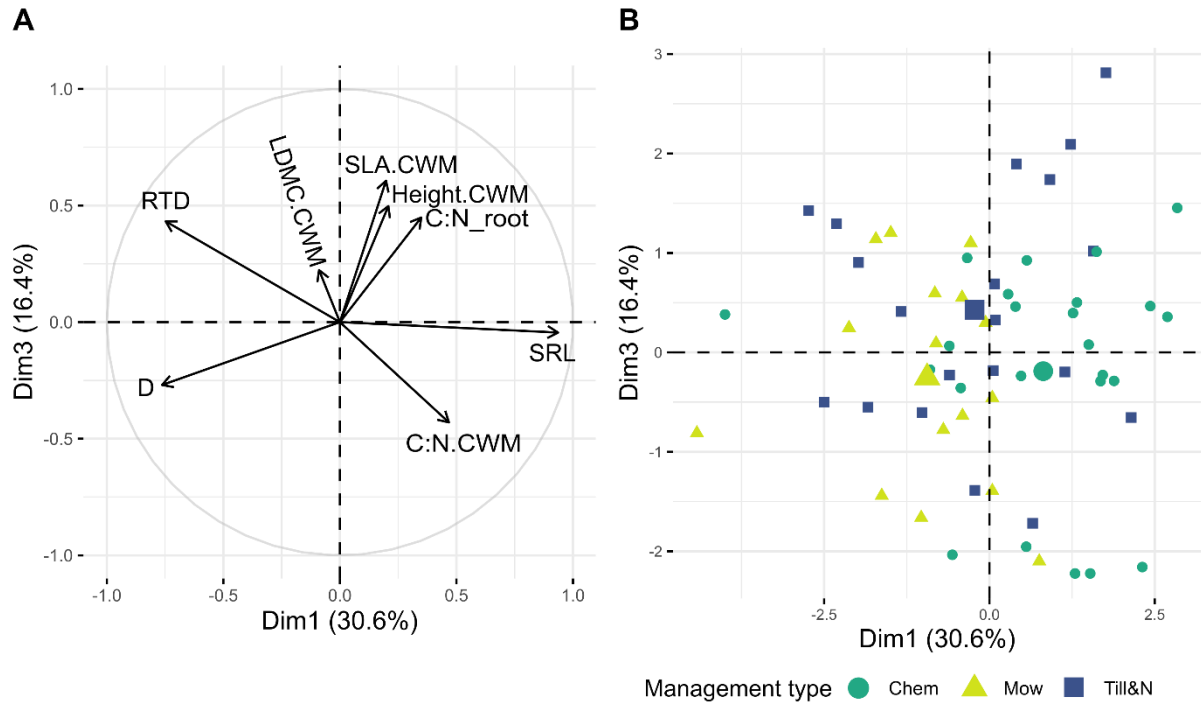


Figure S4 **A** Circle of correlation of the aboveground community weighted means (CWM) and the root traits on the first and third dimensions of the functional PCA. LDMC.CWM, leaf dry matter content ; SLA.CWM, specific leaf area ; C:N.CWM, leaf carbon to nitrogen ratio ; SRL, Specific Root Length ; C:N\_root, carbon to nitrogen ratio of the roots ; RTD, Root Tissue Density ; D, root diameter. **B** Weed community projection in the first and third axes of the functional PCA. Each dot is a weed community whose colour and form refer to weed management.

## SUPPORTING TABLES

*Table S1 Climate and soil characteristics of the vineyard network. Std. Dev., standard deviation.*

<b>Variables</b>	<b>Units</b>	<b>Mean</b>	<b>Std. Dev.</b>	<b>Min</b>	<b>Max</b>
<b>Climate characteristics</b>					
Rainfall	mm	801	123	554	929
Mean temperature	°C	14.8	0.8	13.7	15.9
Aridity index	-	0.66	0.13	0.45	0.82
<b>Soil characteristics</b>					
pH	-	8.2	0.6	6.7	8.8
Clay	%	21.8	7.5	10.7	36.8
Silt	%	36.4	11.1	14.6	63.4
Sand	%	41.8	13.1	17.4	70.4
C:N	g.kg <sup>-1</sup>	10.7	1.5	7.2	13.2
Total limestone	g.kg <sup>-1</sup>	302	251	1	744
Total carbon	g.kg <sup>-1</sup>	47.7	28.6	9.3	95.4
Total organic carbon	g.kg <sup>-1</sup>	11.4	6.1	4.4	28.9
Cation exchange capacity	cmol <sup>+</sup> .kg <sup>-1</sup>	14.9	5.4	6.2	22.2
Soil organic matter	%	1.98	1.05	0.76	5.00
Ammoniacal nitrogen	mg.kg <sup>-1</sup>	1.7	0.9	0.9	4.5
Nitrate nitrogen	mg.kg <sup>-1</sup>	30.3	17.8	11.2	68.2
Total nitrogen	g.kg <sup>-1</sup>	1.1	0.5	0.5	2.4

Table S2 Pairwise correlations between aboveground and belowground functional metrics at the community level. The correlation coefficients of significant correlations are reported in bold. *p*-values were corrected from multiple testing using Holm correction. SRL, Specific Root Length ; RTD, Root Tissue Density ; D, Diameter ; Root C:N, root carbon to nitrogen ratio ; SLA, Specific Leaf Area ; LDMC, Leaf Dry Matter content ; C:N.CWM, leaf carbon to nitrogen ratio.

	RTD	D	Root C:N	SLA.CWM	Height.CWM	LDMC.CWM	C:N.CWM
<b>SRL</b>	<b>-0.71***</b>	<b>-0.72***</b>	0.31	0.15	0.12	-0.04	<b>0.44*</b>
<b>RTD</b>		0.21	0.10	-0.03	0.15	0.05	-0.37
<b>D</b>			-0.28	-0.13	-0.32	0.11	-0.06
<b>Root C:N</b>				0.16	0.24	0.02	<b>0.44*</b>
<b>SLA.CWM</b>					0.14	<b>0.63***</b>	0.04
<b>Height.CWM</b>						-0.06	-0.02
<b>LDMC.CWM</b>							0.14

Table S3 Standardised estimates of the soil abiotic characteristics (pH, SOM, %Sand, soil C:N), climate (aridity index) and management explaining weed functional parameters at the community level (n=15). The selected models of SLA, LDMC, height, root diameter, RTD and root C:N are not presented as no fixed effects were selected. Significant p-values ( $p < 0.05$ ) are in bold. Std. est., standardised beta estimates; Std. err., standardised errors; t, t-value; p, p-value;  $R^2$ ,  $R^2$  adjusted;  $AIC_{full}$ , corrected Akaike information criterion of the full model;  $AIC_{sel}$ , AIC of the selected model; SOM, Soil Organic Matter; SLA, Community Weighted Means of Specific Leaf Area; LDMC, CWM of Leaf Dry Matter Content; SRL, Specific Root Length; RTD, Root Tissue Density.

Explained variables	Explaining variables	Std. est.	Std. err.	t	p	$R^2$	$AIC_{full}$	$AIC_{sel}$
Leaf C:N	(Intercept)	0.75	0.25	7.61	<b>&lt;0.001</b>	63%	91.4	70.3
	Weed management 'Mow' compared to 'Chem'	-1.16	0.42	-2.80	<b>0.017</b>			
	Weed management 'Till&N compared to 'Chem'	-1.33	0.37	-3.61	<b>0.004</b>			
	%Sand	0.43	0.17	2.51	<b>0.029</b>			
SRL	(Intercept)	0.74	0.34	9.79	<b>&lt;0.001</b>	33%	204.1	179.5
	Weed management 'Mow' compared to 'Chem'	-1.48	0.53	-2.79	<b>0.016</b>			
	Weed management 'Till&N compared to 'Chem'	-1.04	0.50	-2.10	0.058			

Table S4 Standardised estimates of the weed functional properties (coordinates of the first two dimensions of the functional PCA) explaining the microbial functional properties (n=60). Significant p-values ( $p < 0.05$ ) are in bold. The full model was composed of the first two dimensions of the functional PCA and the root biomass as fixed effects and a 'vineyard' random effect. Std. est., standardised beta estimates; Std. err., standardised errors; t, t-value; p, p-value;  $R^2_{\text{marg}}$ , marginal  $R^2$ ;  $R^2_{\text{cond}}$ , conditional  $R^2$  ;  $AIC_{\text{full}}$ , corrected Akaike information criterion of the full model ;  $AIC_{\text{sel}}$ , AIC of the selected model ; SIR, Substrate Induced Respiration ; PNEA, Potential Nitrifying Enzyme Activity ; PDEA, Potential Denitrifying Enzyme Activity.

Explained variables	Explaining variables	Std. est.	Std. err.	t	p	$R^2_{\text{marg}}$	$R^2_{\text{cond}}$	$AIC_{\text{full}}$	$AIC_{\text{sel}}$
Microbial biomass (SIR)	(Intercept)	0.67	0.10	12.39	<b>&lt;0.001</b>	0.16	0.10	72.5	52.3
	Root biomass	-0.04	0.03	-1.44	0.16				
Relative abundance of nitrifiers (PNEA:SIR)	(Intercept)	0.96	0.09	10.45	<b>&lt;0.001</b>	0	0.49	-152.2	-187.2
Relative abundance of denitrifiers (PDEA:SIR)	(Intercept)	0.60	0.10	10.15	<b>&lt;0.001</b>	0.01	0.78	128.3	111.4
	Root biomass	0.03	0.05	0.64	0.525				

Table S5 Pairwise correlations between functional properties of microbial communities. The correlation coefficients are reported and the p-values, which were corrected from multiple testing using Holm correction, are detailed in brackets.

	<b>Relative abundance of nitrifiers (PNEA:SIR)</b>	<b>Relative abundance of denitrifiers (PDEA:SIR)</b>
<b>Microbial biomass (SIR)</b>	-0.2 (P=0.28)	-0.05 (P=0.72)
<b>Relative abundance of nitrifiers (PNEA:SIR)</b>		0.26 (P=0.17)
<b>Relative abundance of denitrifiers (PDEA:SIR)</b>		



*Table S6 Dataset of the study at two levels: community level (n=60) and vineyard level (n=15) (EXCEL FILE)*

# SYNTHESE ET DISCUSSION GENERALE



Discussion avec Jacques Maillet sur le terrain

Photo de Guillaume Fried (Hérault, octobre 2020)



Cette partie est constituée de deux sous-parties discutant les deux questions générales de la thèse que nous rappelons ici:

- (i) Quels sont les effets des conditions pédoclimatiques et des pratiques de gestion sur les propriétés fonctionnelles des communautés adventices à différentes échelles spatiales (régionale et nationale) et dans le temps (des années 1980s à 2020s) ?
- (ii) Comment les communautés adventices influencent-elles le recyclage de la matière organique, plus précisément la décomposition et les propriétés fonctionnelles des microorganismes nitrifiants et dénitrifiants ?

# **1. Réponse des communautés adventices des vignobles aux filtres pédoclimatiques et aux pratiques de gestion du couvert**

## **1.1. L'importance relative des filtres pédoclimatiques et agronomiques à différentes échelles spatiales**

En introduction de la thèse, nous avons fait l'hypothèse que **l'importance relative de l'effet des pratiques de gestion des adventices sur les propriétés fonctionnelles des communautés adventices des vignobles serait plus élevée à petite échelle (i.e. régionale) qu'à plus grande échelle (i.e. nationale)**. En synthétisant l'ensemble des résultats des chapitres 1, 2, 4 et 5, **nous validons cette hypothèse** (Figure 23). A l'échelle de trois régions viticoles (chapitre 1), le pédoclimat explique 53% des variations des propriétés fonctionnelles des communautés adventices tandis que les pratiques de gestion des adventices en expliquent 19%. A l'échelle du Bordelais sur un réseau de 100 parcelles viticoles (chapitre 2), les pratiques de gestion expliquent le premier axe de variation de la RLQ (66% de la variance expliquée) tandis que les conditions édaphiques expliquent le deuxième axe (13% de la variance expliquée) (Figure 23). A l'échelle de 16 et 15 parcelles viticoles du

Montpelliérais (chapitre 4 et 5), les pratiques expliquent la majeure partie des variations fonctionnelles des communautés adventices tandis que les conditions édaphiques ont un faible effet et le climat n'en a pas (Figure 23).

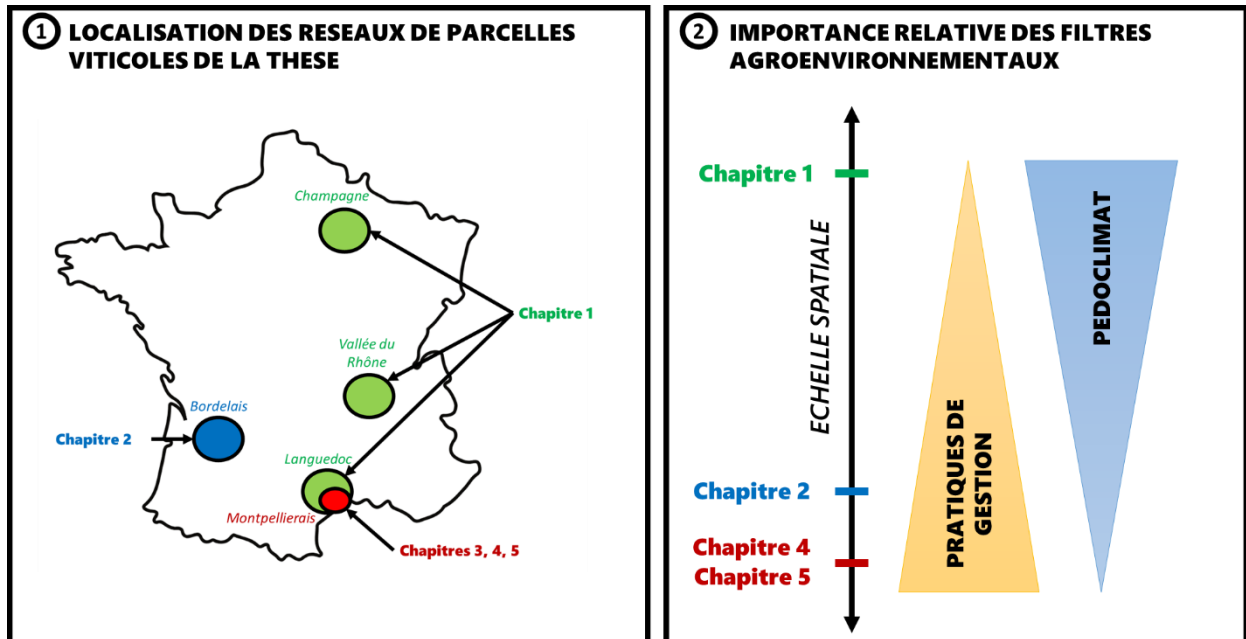


Figure 23 (1) Localisation des réseaux de parcelles viticoles de chaque chapitre de thèse. (2) Importance relative des filtres agroenvironnementaux en fonction de l'échelle spatiale d'étude de chaque chapitre. Le chapitre 3 n'est pas placé sur ce schéma car son approche temporelle ne permet pas d'estimer l'importance relative des filtres d'un point de vue spatial.

## 1.2. L'influence des pratiques de gestion sur les propriétés fonctionnelles des adventices des vignobles

En introduction de la thèse, nous avons formulé plusieurs hypothèses sur la caractérisation de l'intensité des pratiques de gestion des adventices en tant que perturbation et leurs effets sur les propriétés fonctionnelles des communautés adventices :

- (i) Le travail du sol et le désherbage chimique constituent des perturbations plus intenses que la tonte car ces deux pratiques détruisent l'intégralité de la biomasse adventice. Elles

favorisent des communautés adventices adaptées à des milieux très perturbés, rudérales et à stratégie d'acquisition de ressources,

- (ii) La tonte constitue une perturbation moins intense que le travail du sol et le désherbage chimique car elle ne détruit qu'une partie de la biomasse adventice. Elle favorise des communautés adventices moins perturbées, moins rudérales, plus compétitives et à stratégie de conservation de ressources.

### **1.2.1. Le phénotype moyen d'une adventice issue d'une parcelle viticole désherbée chimiquement, travaillée et tondue**

Le Tableau 3 résume les traits fonctionnels et types biologiques des communautés adventices en réponse aux trois pratiques de gestion des adventices étudiées dans la thèse (herbicides, travail du sol et tonte) des chapitres 1, 2, 4 et 5 (le chapitre 3 n'est pas inclus car l'analyse temporelle ne permet pas de renseigner ce type de tableau).

#### *Les propriétés fonctionnelles favorisées par le travail du sol*

En accord avec nos hypothèses, nous avons démontré que le travail du sol favorise des communautés adventices à stratégie acquisitive (teneur en azote foliaire élevée, C:N foliaire faible, Lignine:N foliaire faible), composées d'une grande part de thérophytes et à stratégie rudérale (Tableau 3), en accord avec la littérature (Guerra et al., 2021; Hall et al., 2020; Mainardis et al., 2020). De façon plus surprenante par rapport à nos attendus, le travail du sol a également tendance à favoriser des communautés adventices à masse de graines et à hauteur maximale élevées par rapport aux autres modes de gestion, valeurs de traits qui sont plutôt associées à une stratégie compétitive (Grime, 1977). MacLaren et al. (2019) démontrent également cette association dans les vignobles d'Afrique du Sud. Nous faisons l'hypothèse que le travail du sol favorise des grosses graines car elles ont une meilleure probabilité de germer, lorsqu'elles sont enfouies dans le sol sous l'action du travail (Hernández Plaza et al., 2015). De plus, le travail du sol est associé à des communautés adventices à longueur spécifique racinaire faible et donc à stratégie de collaboration mycorhizienne pour l'acquisition de ressources souterraines. Garcia et al. (2019) ont démontré que le travail du sol

favorise plutôt des communautés adventices et semées à SRL élevé par rapport à la tonte. Pourtant, dans le chapitre 5, l'effet de la tonte et du travail du sol sur le SRL des communautés est similaire.

#### *Les propriétés fonctionnelles favorisées par le désherbage chimique*

Le désherbage chimique favorise des communautés adventices qui ont tendance à avoir une capacité de propagation latérale et une hauteur maximale faibles, qui sont plutôt des valeurs de traits associées à la stratégie rudérale (Tableau 3). Cependant, en contraste avec nos hypothèses et avec la littérature (Hall et al., 2020), le désherbage chimique est associé à des communautés adventices à stratégie de conservation de ressources (faible teneur en azote foliaire, C:N foliaire et Lignine:N foliaire élevés) et ne favorise pas significativement des stratégies rudérales de communautés adventices (Tableau 3).

#### *Les propriétés fonctionnelles favorisées par la tonte*

En accord avec nos hypothèses et la littérature, la tonte favorise des types biologiques non annuels (notamment les hémicryptophytes) et des communautés adventices à stratégie plus compétitive (Hall et al., 2020; Mainardis et al., 2020). Cependant, la tonte est associée à des communautés à stratégie acquisitive à l'échelle régionale (teneur en azote foliaire élevée, C:N foliaire faible, Lignine:N foliaire faible, teneur en hémicellulose faible), ce qui contraste avec la majorité des études sur les communautés adventices en vignobles (Guerra et al., 2021; Hall et al., 2020; Kazakou et al., 2016; Mainardis et al., 2020).

#### *Le phénotype moyen d'une adventice d'une communauté issue d'une parcelle désherbée comparé à celui d'une adventice d'une communauté provenant de parcelles viticoles travaillées et tondues*

En rassemblant l'ensemble de ces résultats hétérogènes de par l'échelle spatiale des études (nationale et régionale) et de par l'origine des valeurs de traits sur lesquelles elles se basent (mesurées pendant la thèse ou exportées d'une base de données internationale comme TRY), nous proposons la synthèse suivante: **le désherbage chimique favorise des communautés adventices à stratégie foliaire de conservation des ressources, peu compétitives pour l'espace et les ressources aériennes et ayant un potentiel élevé d'exploration des ressources du sol.** Selon cette hypothèse, **la stratégie aérienne des communautés adventices désherbées chimiquement est plutôt stress-tolérante**

tandis que la stratégie racinaire est explorative des ressources du sol. La Figure 24 propose un schéma du phénotype moyen d'une adventice issue d'une communauté d'une parcelle dés herbée chimiquement. Au contraire, les adventices des communautés issues de parcelles travaillées et tondues ont une stratégie aérienne d'acquisition de ressources et une stratégie racinaire d'acquisition de ressources basée sur la collaboration avec les mycorhizes du sol (Figure 24).

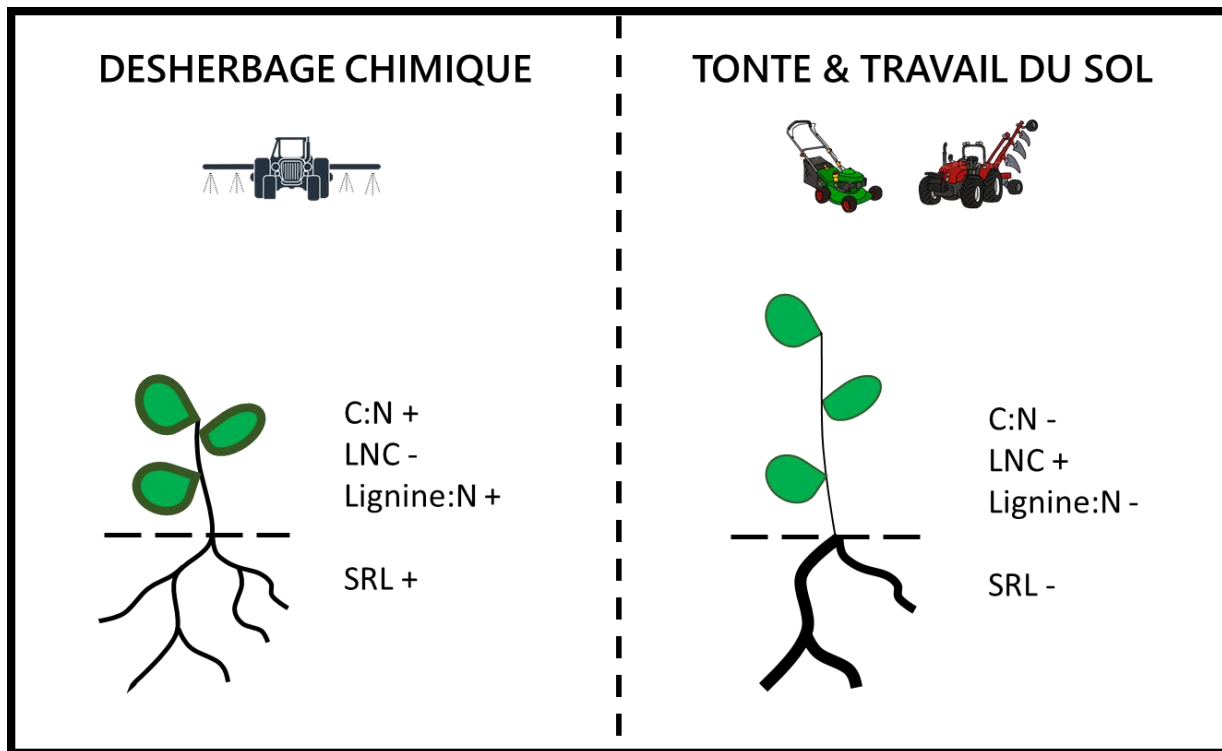


Figure 24 Le phénotype moyen schématique d'une adventice d'une parcelle dés herbée chimiquement comparé aux phénotypes moyens des adventices d'une parcelle travaillée et tondue, selon les résultats de la thèse (chapitre 4 et 5). C:N, ratio carbone sur azote foliaire, LNC, teneur en azote foliaire, Lignine:N, ratio lignine et azote foliaire ; SRL, longueur racinaire spécifique.

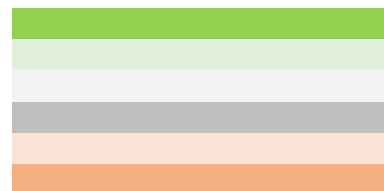


Tableau 3 Propriétés fonctionnelles des communautés adventices en réponse aux trois pratiques de gestion des couverts étudiées dans la thèse (herbicides, travail du sol et tonte) issus des résultats des différents chapitres de la thèse. Pour chaque trait, un code couleur indique le signe des relations pratiques-propriétés fonctionnelles (rouge, négatif ; gris, relation non significative ; vert, positif). Le chiffre inscrit au centre de la case dénombre le nombre de réseaux de parcelles viticoles corroborant le résultat. Les nuances sont plus intenses si les résultats ont été démontrés dans la majorité des réseaux de parcelles viticoles de la thèse (voir légende ci-dessous pour plus de précisions). Les chapitres de thèse correspondants sont reportés dans la colonne de droite. Les réseaux viticoles dénombrés sont les suivants: le réseau du Languedoc Roussillon, de Champagne, de la Vallée du Rhône, le réseau regroupant tous ces réseaux à l'échelle nationale (les résultats ne sont pas les mêmes qu'à l'échelle régionale), le réseau du Bordelais et le réseau « Processus » du Montpelliérais

		Herbicides	Travail	Tonte	Chap. de thèse
Traits foliaires	SLA	6	6	5 1	1, 2, 5
	LDMC	2	2	1 1	4, 5
	LNC	1	1	1	4
	C:N foliaire	1	1	1	4, 5
	Cellulose	1	1	1	4
	Hemicellulose	1	1	1	4
	Lignine	1	1	1	4
	Lignine:N	1	1	1	4
Traits racinaires	SRL	1	1	1	5
	C:N racinaire	1	1	1	5
	Diamètre racinaire	1	1	1	5
	RTD	1	1	1	5
Phénologie	Début de floraison	4 1	4 1	4 1	1, 2
	Durée de floraison	4 1	3 1 1	4 1	1, 2
Reproduction	Masse de graines	4 1	3 2	4 1	1, 2
	Propagation latérale	2 2	2 2	3 1	1
Trait plante entière	Hauteur	2	2	2	2, 5
	Hauteur maximale	2 1 1	2 2	3 1	1
Stratégie de Grime	C	1	1	1	2
	S	1	1	1	2
	R	1	1	1	2
Classification de Raunkiaer	Thérophyte	1	1	1	2
	Hémicryptophyte	1	1	1	2

#### Légende

Effet positif démontré dans au moins 2 réseaux de parcelles viticoles de la thèse  
 Faible effet positif démontré dans 1 réseau de parcelles viticoles de la thèse  
 Absence d'effet démontré dans 1 réseau de parcelles viticoles de la thèse  
 Absence d'effet dans au moins 2 réseaux de parcelles viticoles de la thèse  
 Faible effet négatif démontré dans 1 réseau de parcelles viticoles de la thèse  
 Effet négatif démontré dans au moins 2 réseaux de parcelles viticoles de la thèse



### **1.2.2. La variabilité fonctionnelle de communautés adventices issues de parcelles viticoles désherbées chimiquement, travaillées et tondues**

Le Tableau 4 résume la réponse de la variabilité fonctionnelle à l'échelle de la communauté aux pratiques de gestion qui a été explorée dans deux chapitres de thèse (1 et 4) et dans 4 réseaux de parcelles viticoles (Champagne, Vallée du Rhône, Languedoc-Roussillon et réseau 'Processus' de 16 parcelles du Montpelliérais). Les indices de variation fonctionnelle de distribution des valeurs de traits au sein des communautés sont différents selon les chapitres de thèse: community weighted variances pour le chapitre 1 et les indices de RaoQ pour le chapitre 4 (cf introduction générale de la thèse, paragraphe 3.3). **Nous avons émis l'hypothèse que les communautés adventices issues de parcelles désherbées et travaillées sont des communautés à plus faible diversité fonctionnelle que celle des communautés adventices issues de parcelles tondues car le désherbage chimique et le travail constituent des perturbations plus intenses que la tonte.**

En accord avec notre hypothèse, le désherbage chimique est associé à des communautés adventices à faible diversité fonctionnelle, qui convergent vers des valeurs élevées de C:N foliaire, de lignine:N foliaire et de faibles valeurs d'azote foliaire (Figure 25, Tableau 4). Au contraire, le travail du sol est associé à une diversité plus élevée de C:N, de lignine:N foliaires et de teneur en azote au sein des communautés adventices (chapitre 4, Figure 25, Tableau 4) tandis que la diversité fonctionnelle des communautés adventices issues de parcelles viticoles tondues n'est pas significativement différente des autres modes de gestion. Ces résultats contrastent avec les résultats de Kazakou et al., (2016) et Mainardis et al. (2020) qui démontrent que les valeurs de diversité fonctionnelle sont plus élevées chez les communautés issues de parcelles tondues que de parcelles travaillées. Quelques effets confondants peuvent expliquer ces résultats : la fertilisation était plus élevée dans les communautés travaillées que dans les communautés désherbées chimiquement. Les parcelles viticoles travaillées étaient donc caractérisées par une intensité de perturbation élevée mais également par un niveau en ressources azotées élevé. Niu et al. (2014) ont démontré que la fertilisation accroît la diversité fonctionnelle des communautés prairiales car elle favorise la coexistence de différentes stratégies fonctionnelles dans un environnement où la compétition azotée est limitée par un niveau plus élevé de nutriments.

Tableau 4 Réponse des variations de distribution de valeurs de chaque trait à l'échelle de la communauté aux pratiques de gestion étudiées dans la thèse (herbicides, travail du sol et tonte) issus des résultats des différents chapitres de la thèse. Pour chaque trait, un code couleur indique le signe des relations pratiques-variances fonctionnelles (rouge, négatif ; gris, relation non significative ; vert, positif). Les nuances sont plus intenses si les résultats ont été trouvés dans la majorité des chapitres (voir légende ci-dessous pour plus de précisions). Le indices de variances fonctionnelles ne sont pas les mêmes selon les chapitres. Les chapitres de thèse correspondants sont reportés dans une colonne. Dans le chapitre 1, il s'agit des Community Weighted Variances, corrigées par la richesse spécifique. Dans le chapitre 4, il s'agit des coordonnées des communautés adventices dans un espace fonctionnel d'indice de RaoQ de chaque trait.

		Herbicides		Travail		Tonte		Chap. de thèse
Traits foliaires	SLA	2	1	2	1	2	1	1
	LNC	1		1		1		4
	C:N foliaire	1		1		1		4
	Hemicellulose	1		1		1		4
	Lignine	1		1		1		4
	Lignine:N	1		1		1		4
Phénologie	Début de floraison	2	1	2	1	2	1	1
	Durée de floraison	2	1	2	1	2	1	1
Reproduction	Masse de graines	3		3		3		1
	Propagation latérale	2	1	2	1	3		1
Trait plante entière	Hauteur maximale	3		3		3		1

**Légende**

Effet positif démontré dans au moins 2 réseaux de parcelles viticoles de la thèse

Faible effet positif démontré dans 1 réseau de parcelles viticoles de la thèse

Absence d'effet démontré dans 1 réseau de parcelles viticoles de la thèse

Absence d'effet dans au moins 2 réseaux de parcelles viticoles de la thèse

Faible effet négatif démontré dans 1 réseau de parcelles viticoles de la thèse

Effet négatif démontré dans au moins 2 réseaux de parcelles viticoles de la thèse



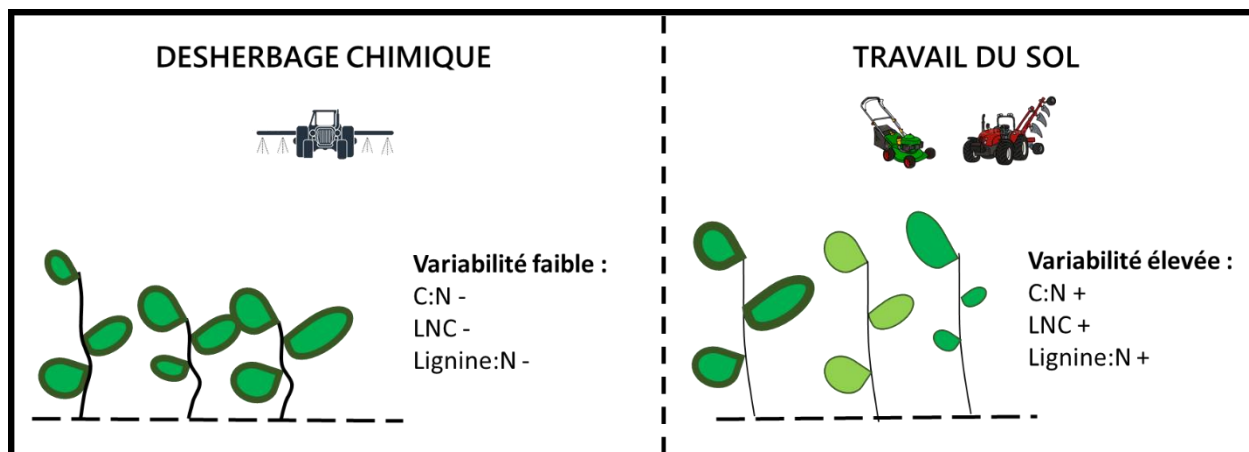


Figure 25 Variabilité fonctionnelle des communautés issues de parcelles désherbées et des communautés issues de parcelles travaillées, selon les résultats du chapitre 4. C:N, ratio carbone sur azote foliaire, LNC, teneur en azote foliaire, Lignine:N, ratio lignine et azote foliaire

Nos résultats démontrent que les communautés adventices issues de parcelles travaillées se caractérisent par des propriétés fonctionnelles foliaires et racinaires plus semblables aux communautés adventices issues de parcelles tondues qu'à celles issues de parcelles désherbées chimiquement. Le désherbage chimique favorise des communautés convergentes, à stratégies aériennes stress-tolérantes, de conservation de ressources et d'exploration racinaire des ressources du sol tandis que la tonte et le travail sont associées à des propriétés fonctionnelles opposées. Ces résultats remettent en cause notre classification de l'intensité des pratiques de sol (tonte < désherbage chimique et travail) (cf introduction générale de la thèse, paragraphe 3.2.2).

## 1.3. Les adventices des vignes, des rudérales ?

### 1.3.1. A l'échelle spécifique, les espèces adventices observées dans les vignobles du Montpelliérais couvrent une large gamme des stratégies CSR définies par Grime

Historiquement, les adventices ont été définies par leurs capacités à persister dans un milieu perturbé et leurs stratégies rudérales (Baker, 1965; Grime, 1974). En introduction, nous avons

émis l'hypothèse que les adventices des milieux viticoles étaient localisées près du sommet « R » du triangle de Grime (Figure 3). La Figure 26 présente la localisation des adventices des 40 parcelles du Montpelliérais (réseau historique 'Maillet' du chapitre 3) dans le triangle CSR. Contrairement à notre hypothèse initiale, **les adventices couvrent une grande partie du triangle de Grime à l'échelle spécifique**: du coin « R » (R-score maximal à 96% pour *Galium aparine*), au coin « S » (S-score maximal à 95% pour *Misopates orontium*) au coin « C » (C-score maximal à 85% pour *Cirsium vulgare*) (Tableau 5). Trente-huit pourcent des adventices ont un score de stress tolérance nul et se trouvent entre les sommets C et R en bordure gauche du triangle. Les adventices les plus abondamment observées dans les parcelles viticoles sont globalement réparties dans la moitié basse du triangle (C-score < 50%). Certaines sont effectivement rudérales comme *Veronica persica*, mais d'autres sont stress-tolérantes comme *Vulpia ciliata* ou encore *Anacyclus radiatus*. *Diplotaxis eruroides* est l'une des adventices les plus abondantes ayant le score de compétitivité le plus élevé (45%). L'étude de Guerra et al., (2021) a également démontré la grande diversité de stratégies CSR des adventices des agroécosystèmes viticoles méditerranéens avec 29 espèces, recouvrant une large gamme du triangle. Les positions des espèces abondantes quantifiées par Guerra et al. (2021) sont d'ailleurs très comparables à celles des adventices observées dans le Montpelliérais. Cette grande diversité de stratégies CSR des adventices est-elle spécifique à la vigne ou se vérifie-t-elle également dans les agroécosystèmes annuels ? Le spectre biologique de la vigne est plus varié que dans les cultures annuelles (plus de pérennes présentes en vigne que dans les cultures annuelles) et suppose donc déjà une moindre dominance des rudérales. Si l'on prend des espèces annuelles communes à toutes les cultures (par exemple, *Papaver rhoeas*, *Stellaria media*, *Galium aparine*, abondantes en vigne et en blé) (Fried et al., 2012), leurs stratégies pourraient être différentes et plus variées en vignes, en réponse à la plus grande diversité des modes de gestion des adventices : la variabilité intraspécifique peut aussi expliquer une partie de nos observations.

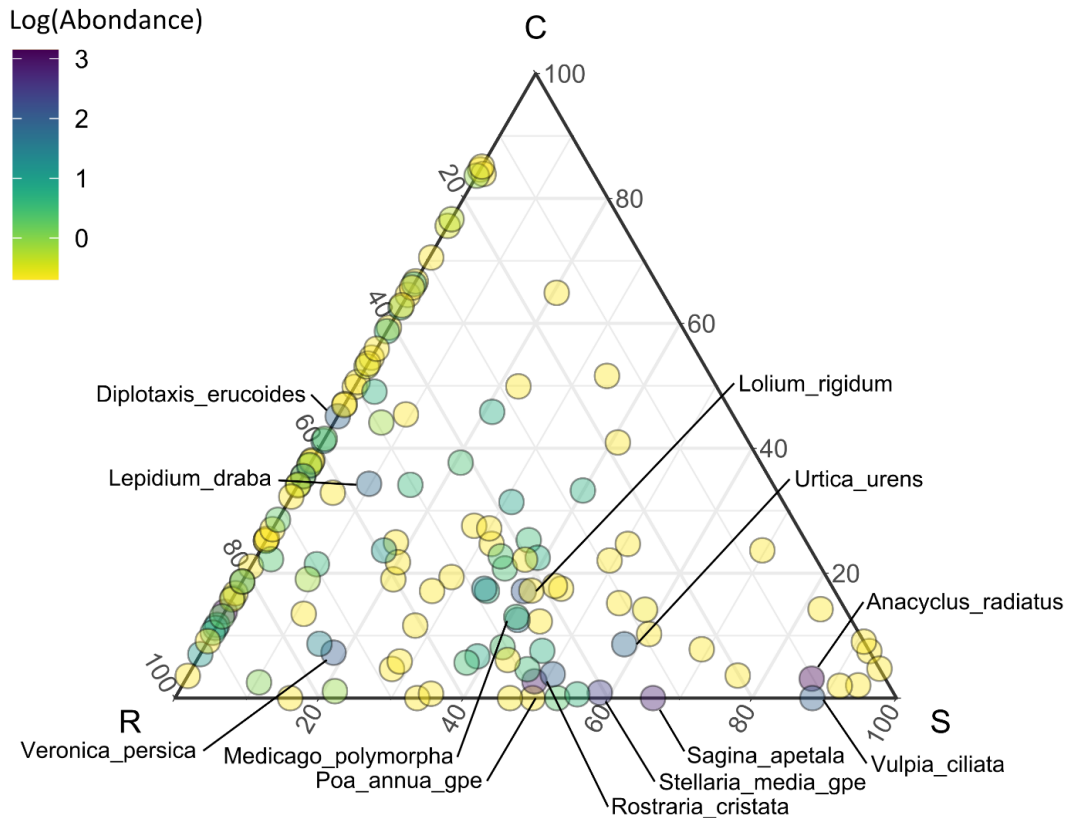


Figure 26 Stratégies CSR des adventices identifiées, en mars, juin et octobre 2020 et 2021, dans 40 parcelles du Montpelliérais. Chaque rond représente une adventice. Le gradient de couleur du jaune au violet représente le gradient des moyennes d'abondances loguées de chaque adventice (moyenne sur les 6 relevés 2020-2021). Les valeurs de traits utilisés pour définir les stratégies de chaque adventice (en utilisant l'algorithme de Pierce et al., 2017) ont été mesurées dans des vignes gérées par des pratiques différentes. C'est la position moyenne de cette espèce qui est représentée ici.

Tableau 5 Statistiques descriptives des scores CSR des espèces adventices observées dans le Montpelliérais (réseau historique 'Maillet' sur 40 parcelles en mars, juin, octobre 2020 et 2021).

Statistiques descriptives	Score R (rudéralité)	Score C (compétitivité)	Score S (tolérance au stress)
Moyenne	49%	27%	23%
Ecart-type	23%	22%	27%
Maximum	96%	85%	95%
Minimum	0%	0%	0%
Coefficient de variation: écart-type/moyenne	46%	82%	111%

### **1.3.2. Les communautés adventices viticoles observées dans la thèse couvrent une large gamme des stratégies CSR**

Qu'en est-il au niveau des communautés ? La Figure 27 représente le score CSR des communautés adventices de la thèse issues des différentes régions d'études: la Champagne, la Vallée du Rhône et l'ancien Languedoc-Roussillon (chapitre 1) et le Montpelliérais (réseau historique Maillet de 40 parcelles du chapitre 3). En moyenne, les communautés ont un score de rudéralité de 52% +/- 10, un score de compétitivité de 31% +/- 10 et un score de tolérance au stress de 18% +/-12 (Tableau 6). Si l'ensemble des communautés se situent plutôt vers la partie gauche du triangle, entre les sommets R et C, elles recouvrent une large partie du triangle (environ 40% si on estime que les communautés se situent dans un triangle équilatéral de 65% de longueur de côté). Les communautés adventices sur lesquelles se base la thèse se distinguent entre elles par une grande variabilité de scores S-tolérantes (coefficient de variation de 66%). Un groupe composé de 16% de l'ensemble des communautés adventices a un score de stress tolérance nul et se situe en bordure de triangle entre les sommets R et C tandis que certaines communautés ont des S-scores élevés, de l'ordre de 50% (Tableau 6). Les communautés adventices sont moins hétérogènes entre elles pour le score C (coefficient de variation de 32%) et homogènes sur le score R (coefficient de variation de 18%) (Tableau 6). L'étude de Guerra et al. (2021) démontre une plus grande diversité de stratégies CSR des communautés adventices des vignobles méditerranéens, en réponse aux pratiques de gestion des adventices et sur un nombre réduit de site d'études (8 sites). Si les communautés adventices sont majoritairement rudérales, leurs stratégies CSR recouvrent néanmoins une large gamme du triangle. **Cette large gamme de stratégies CSR chez les communautés adventices des agroécosystèmes viticoles interroge la définition conceptuelle des pratiques de gestion des adventices en tant que perturbation.**

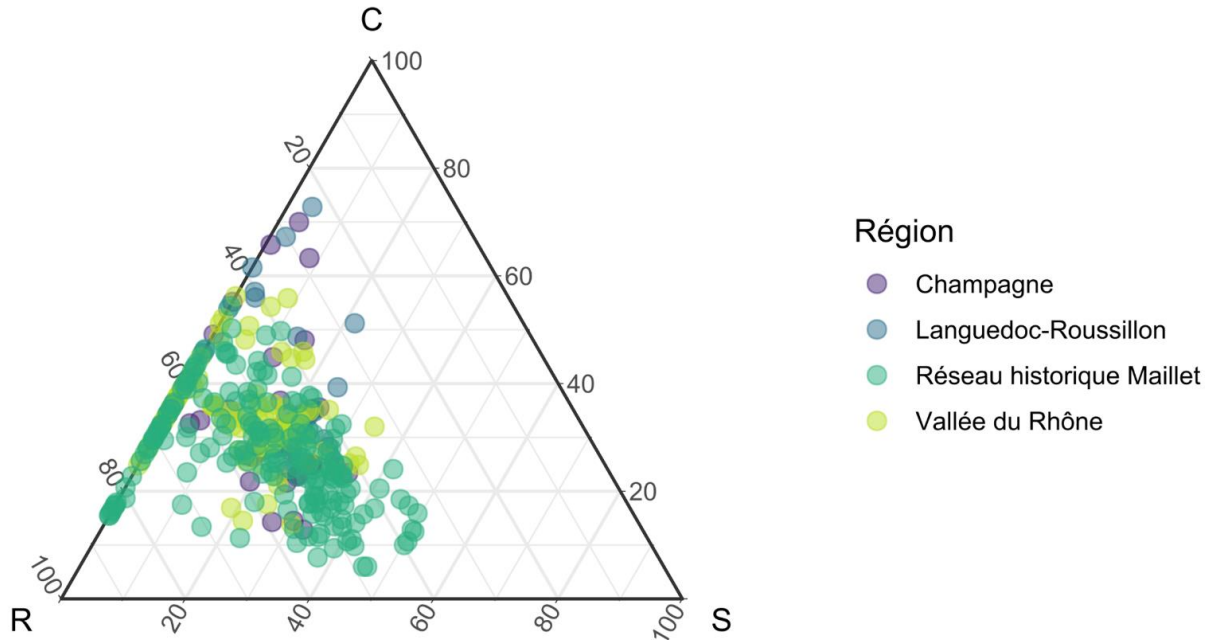


Figure 27 Score CSR des communautés adventices du chapitre 1 (Champagne, Vallée du Rhône et Languedoc Roussillon ; observées à la sortie d’hiver, en début d’été et en automne de 2006 à 2012) et les communautés adventices du réseau Maillet de 40 parcelles de vigne (observées en mars, juin, octobre 2020 et 2021) (chapitre 3). Chaque point représente le score CSR d’une communauté. Sa couleur est associée à la région où cette communauté est localisée. Au total, 461 communautés sont représentées dans le triangle

Tableau 6 Statistiques descriptives des scores CSR des communautés adventices de la thèse issues des relevés floristiques effectués en Champagne, en Vallée du Rhône, en Languedoc-Roussillon et dans le Montpelliérais (réseau « Maillet »).

Statistiques descriptives	Score R (rudéralité)	Score C (compétitivité)	Score S (tolérance au stress)
Moyenne	52%	31%	18%
Ecart-type	10%	10%	12%
Maximum	85%	73%	51%
Minimum	23%	6%	0%
Coefficient de variation: écart-type/moyenne	18%	32%	66%



## **1.4. Les pratiques de gestion des adventices des vignobles: des filtres difficilement caractérisables méthodologiquement et conceptuellement**

### **1.4.1. La caractérisation méthodologique des pratiques de gestion des adventices des agroécosystèmes viticoles**

Plusieurs systèmes de caractérisation des pratiques ont été employés dans les chapitres de thèse. Dans le chapitre 1 à l'échelle nationale, une approche par gradient de pratiques a été utilisée, basée sur un système de variables quantitatives décrivant le nombre de passages (nombre de passage de désherbage chimique, de travail du sol ou de tonte) puis une analyse multivariée de ces variables pour identifier des gradients de variation de pratiques au sein des réseaux viticoles. Dans le chapitre 3 à l'échelle régionale, dû au manque de précision de l'historique culturelle des années 1980 à 2020, des variables binaires « oui/non » ont été associées à l'emploi des herbicides, l'utilisation du travail du sol ou de la tonte. Dans le chapitre 4 et 5 à l'échelle régionale, une variable qualitative décrivant le type de pratique majoritaire (désherbage chimique/travail/tonte) a été choisie sur la base d'une classification ascendante hiérarchique des pratiques des viticultrices et viticulteurs. Cette simplification de la caractérisation des pratiques le long de la thèse provient de l'échelle de plus en plus petite d'exploration des relations pratique-traits (nationale à régionale), de la réduction du nombre de parcelles viticoles et d'une diversité de pratiques plus réduites (en termes de type de pratique, de fréquence et d'intensité); mais aussi peut-être de l'oubli progressif du coût<sup>7</sup> des entretiens auprès de viticulteurs et viticultrices, peu disponibles (les chapitres de thèse étant globalement dans l'ordre temporel de traitement lors de la thèse). De mon point de vue, cette simplification progressive a rendu les résultats plus clairs et plus communicables.

Pour illustrer l'importance du choix du type de variables utilisées, la Figure 28 présente la réponse de la hauteur maximale agrégée à l'échelle de la communauté aux pratiques de gestion, caractérisées par une approche gradient et une approche catégorie de pratique. Dans la Figure 28A,

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<sup>7</sup> Des coûts en termes de temps, d'énergie et pour certains entretiens – d'abnégation

les variables de pratique de gestion des adventices sont caractérisées par un gradient de mode de gestion allant de parcelles viticoles désherbées chimiquement fréquemment à des parcelles viticoles étant travaillées fréquemment. La hauteur maximale agrégée est corrélée significativement à ce gradient, certes à la marge, mais la p-value est bien inférieure à 0.05 (rho: 0.41, P-val: 0.02, résultats issus du chapitre 1). Dans la Figure 28B, les variables de pratique de gestion des adventices sont des variables catégorielles, issues d'une clusterisation des parcelles viticoles gérées similairement (même jeu de données, mêmes variables « brutes » initiales). Quatre groupes de parcelles ont ainsi été définies: celles désherbées chimiquement, celles tondues, celles travaillées et celles gérées avec une stratégie mixte (combinaison de désherbage chimique, tonte et travail du sol). Sur la base de cette caractérisation de pratiques de gestion des adventices, aucune différence significative de hauteur maximale selon les modes de gestion n'est détectée (une tendance visuelle semble se dégager mais non significative), au contraire de la corrélation significative démontrée par l'approche gradient. **Cet exemple montre bien que le choix des variables de pratiques est crucial dans l'analyse et l'interprétation des résultats.**

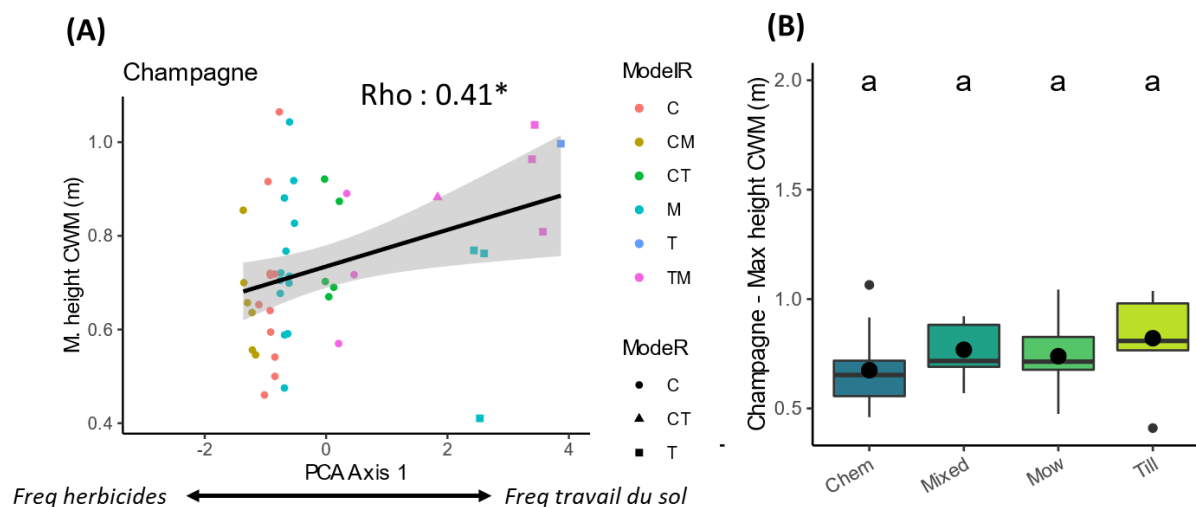


Figure 28 Illustration de l'importance du choix des variables de pratiques. A) Le corrélation entre un axe de pratique (du désherbage chimique au travail du sol) et la hauteur maximale agrégée à l'échelle de la communauté (résultats du chapitre 1). Chaque point est une communauté et la forme et la couleur de chaque point reflète la gestion du rang et de l'inter-rang respectivement. Le coefficient de corrélation est indiqué sur le graphe. C, désherbage chimique ; CM, combinaison de désherbage chimique et de tonte ; CT, combinaison de désherbage chimique et de travail du sol ; M, tonte ; T, travail du sol ; combinaison de travail du sol et de la tonte. B) Influence du mode de gestion principal des adventices sur la hauteur maximale agrégée à l'échelle des communautés. Aucune différence significative n'est détectée. Chem, désherbage chimique ; Mixed, combinaison de désherbage chimique, travail et tonte ; Mow, tonte ; Till, travail du sol.

Au sein des différents chapitres de thèse, nous avons choisi de caractériser les pratiques de gestion du sol par type (désherbage chimique/travail/tonte), et ensuite d'assigner la fréquence de passages par pratique. **Ce choix provient de l'hypothèse implicite que le mécanisme de destruction des adventices a une plus grande influence sur les propriétés fonctionnelles des communautés adventices que la fréquence de destruction.** Cependant, nous n'avons jamais testé cela explicitement. Les Figure 29 et Figure 31 présentent les stratégies CSR des communautés adventices du Montpelliérais (réseau « Maillet »), observées en mars, juin et octobre 2020 et 2021 (40 parcelles). La Figure 29 et la Figure 30 présentent l'effet du type de pratique de gestion des adventices sur les stratégies CSR. Dans le Montpelliérais, les communautés adventices tondues sont plus stress-tolérantes (26% de S-score en moyenne) que les communautés issues de parcelles viticoles travaillées (8% de S-score) (Figure 30). Les communautés adventices issues de parcelles tondues sont également moins rudérales (47% de R-score en moyenne) que les communautés issues de parcelles travaillées (67% de R-score) et désherbées chimiquement (53% de R-score) (Figure 30). Au contraire, si on ne prend plus explicitement le type de pratique comme facteur explicatifs (désherbage chimique, travail, tonte) et uniquement le nombre de passages (toute pratique confondue), il n'y a pas de différences significatives de stratégies CSR des communautés adventices gérées par de fréquents passages ou moins fréquents passages (Figure 31). **Ces résultats valident l'hypothèse que le type de mécanisme de destruction a un effet majeur sur les propriétés fonctionnelles des communautés adventices plutôt que la fréquence de destruction.**

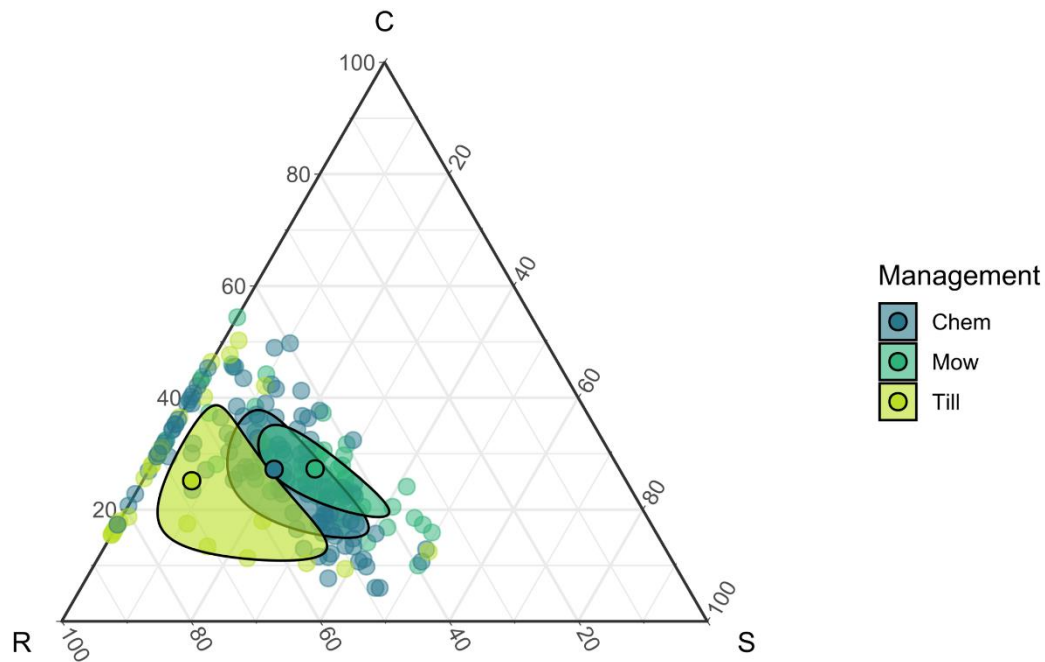


Figure 29 L'effet du type de pratiques de gestion des adventices sur les stratégies CSR des communautés adventices du Montpellierais. Chaque point est une communauté d'adventices. Les couleurs des points représentent le type de pratique de gestion principalement utilisé dans les parcelles. Chem, désherbage chimique ; Mow, tonte ; Till, travail. (Jeu de données Montpellierais, 40 parcelles, 6 relevés floristiques effectués en mars, juin, octobre 2020 et 2021).

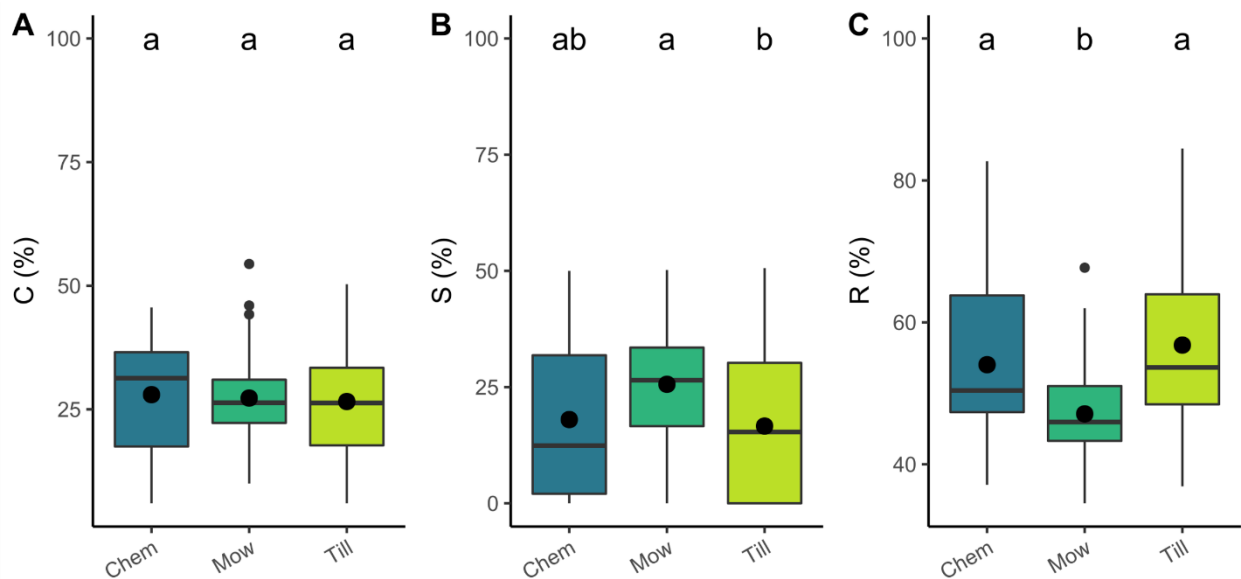


Figure 30 Les stratégies CSR des communautés adventices en fonction du type de pratique de gestion dominant effectué dans les parcelles de vigne. Chem, désherbage chimique ; Mow, tonte ; Till, travail. (Jeu de données Montpellierais, 40 parcelles, 6 relevés floristiques effectués en mars, juin, octobre 2020 et 2021).

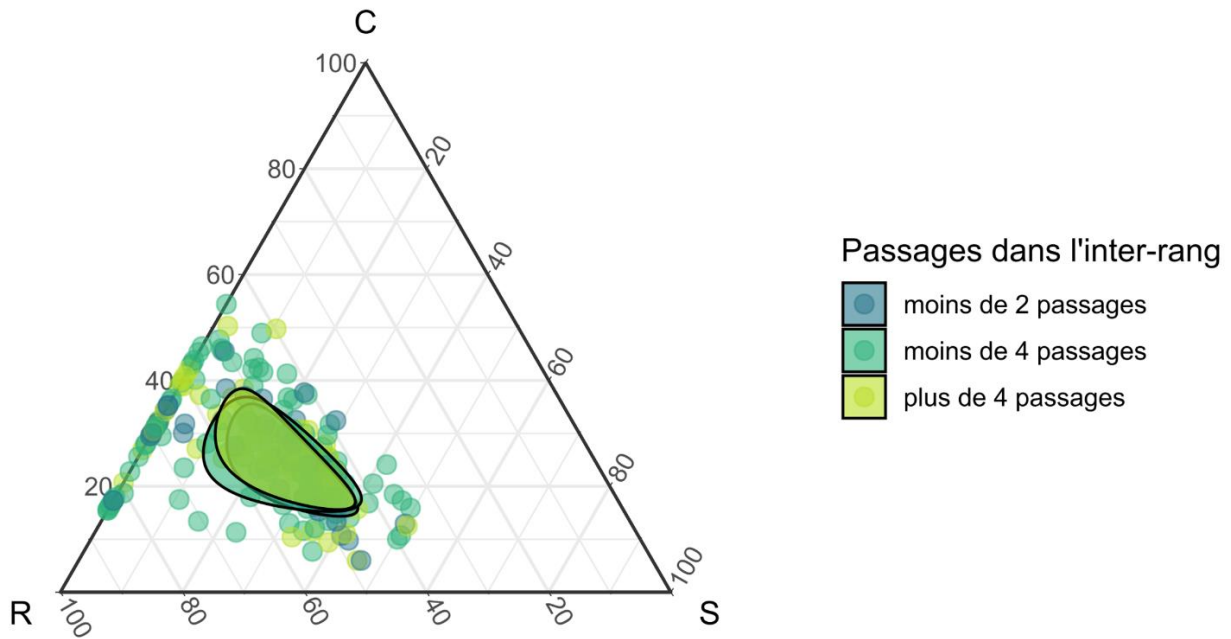


Figure 31 L'effet du nombre de passages toute pratique confondue, sur les stratégies CSR des communautés adventives 2020-2021 dans le Montpellierais. Les couleurs des points représentent le nombre de passage de pratiques. (Jeu de données Montpellierais, 40 parcelles, 6 relevés floristiques effectués en mars, juin, octobre 2020 et 2021).

## 1.4.2. La caractérisation conceptuelle des pratiques de gestion des adventives

### 1.4.2.1. Le désherbage chimique: un stress plus qu'une perturbation?

L'importance du mécanisme de destruction des adventives (soit le type de pratique employé) plutôt que la fréquence de destruction des adventives ainsi que les tableaux de synthèse des résultats de la thèse sur la réponse des communautés adventives aux pratiques de gestion (Tableau 3, Tableau 4) remettent en cause la caractérisation conceptuelle des pratiques de gestion des adventives. **Nous avons fait l'hypothèse que le désherbage chimique et le travail du sol constituaient des perturbations à intensité égale puisque ces deux pratiques détruisent l'intégralité de la biomasse.** En effet, les pratiques de gestion des adventives sont classiquement conceptualisées en perturbation (Gaba et al., 2014), c'est-à-dire un mécanisme qui limite la biomasse des plantes en causant leur destruction partielle ou totale (Grime, 1977). Or, **les résultats de la thèse démontrent une nette différence de structure fonctionnelle des communautés issues des parcelles désherbées et travaillées** (Tableau 3, Tableau 4), que ce soit sur les **stratégies moyennes des**

**communautés adventices** (Tableau 3, Figure 24) et **la diversité de stratégies (ou la diversité fonctionnelle) issue de ces parcelles gérées selon ces deux pratiques** (Tableau 4, Figure 25). Le désherbage chimique favorise notamment au sein du chapitre 4 une stratégie foliaire de conservation de ressources (teneur en C:N, Lignine:N élevées notamment) tandis que la stratégie racinaire est plutôt exploratoire et acquisitive (SRL élevée). Cette stratégie aérienne, pouvant s'apparenter à une stratégie plutôt tolérante au stress, remet en cause la conceptualisation du désherbage chimique en tant que « perturbation ». Selon, Lichtenthaler (1998), les herbicides constituent un stress, défini comme une contrainte externe qui limite le taux de production de matière sèche d'une partie ou de l'ensemble d'une plante (Grime, 1977). Si le stress est très intense, il peut conduire à la mort de la plante. Selon Lichtenthaler (1998), "stress is a dose-dependent matter" (Lichtenthaler, 1988), tout comme l'efficacité d'un herbicide. En effet, si la dose d'herbicide apportée à la parcelle est trop faible, certains herbicides peuvent avoir des effets opposés et stimuler la croissance des plantes (Lichtenthaler, 1998). De plus, contrairement aux perturbations définies comme une destruction non sélective d'une biomasse végétale (Grime, 1977), les herbicides sont sélectifs, y compris les herbicides à large spectre d'action comme le glyphosate. En effet, si la majorité des adventices sont sensibles aux herbicides, certaines adventices peuvent présenter des tolérances ou des résistances. Par exemple, *Malva sylvestris* est naturellement tolérante au glyphosate (Michael et al., 2009) tandis qu'un mécanisme de translocation du glyphosate vers les pointes des feuilles confère une résistance au produit chez certaines populations résistantes de *Lolium rigidum* (Lorraine-Colwill et al., 2002). **L'ensemble de ces considérations semblent indiquer que le désherbage chimique impose un stress aux communautés adventices.**

#### *1.4.2.2. Les propriétés fonctionnelles moyennes d'une adventice désherbée chimiquement: une proposition de modèle hypothétique mécaniste*

Si l'on considère que le désherbage chimique constitue un stress, une autre interprétation peut être avancée pour comprendre le phénotype moyen d'une adventice issue d'une communauté d'une parcelle viticole désherbée chimiquement (Figure 32). Le rapport C:N foliaire élevé des communautés issues de parcelles viticoles désherbées chimiquement peut être dû à une adaptation de la structure foliaire pour diminuer l'absorption des herbicides. En effet, le C:N foliaire est corrélé

positivement avec l'épaisseur de la cuticule (Zukswert and Prescott, 2017) et celle-ci diminue l'absorption du glyphosate (Santier et Chamel, 1992). De plus, un des mécanismes de résistance au glyphosate est de transloquer le glyphosate absorbé par les feuilles vers les racines. L'hypothèse de ce mécanisme de résistance a notamment été émise pour *Poa annua* (Barua et al., 2022; Cross et al., 2015), une espèce adventice très abondante dans les communautés issues de parcelles viticoles désherbées chimiquement du réseau « Processus » (26% du taux de couverture de ces communautés) (chapitre 3 et 4). La translocation importante du glyphosate vers les racines suggère que le glyphosate puisse être exsudé dans le sol, facilité par le rapport longueur sur masse sèche des racines élevé, entraînant ainsi un mécanisme de détoxification au niveau de la plante. Cependant, ce mécanisme d'exsudation n'a pas encore été démontré pour *Poa annua* (Brunharo et al., 2019).

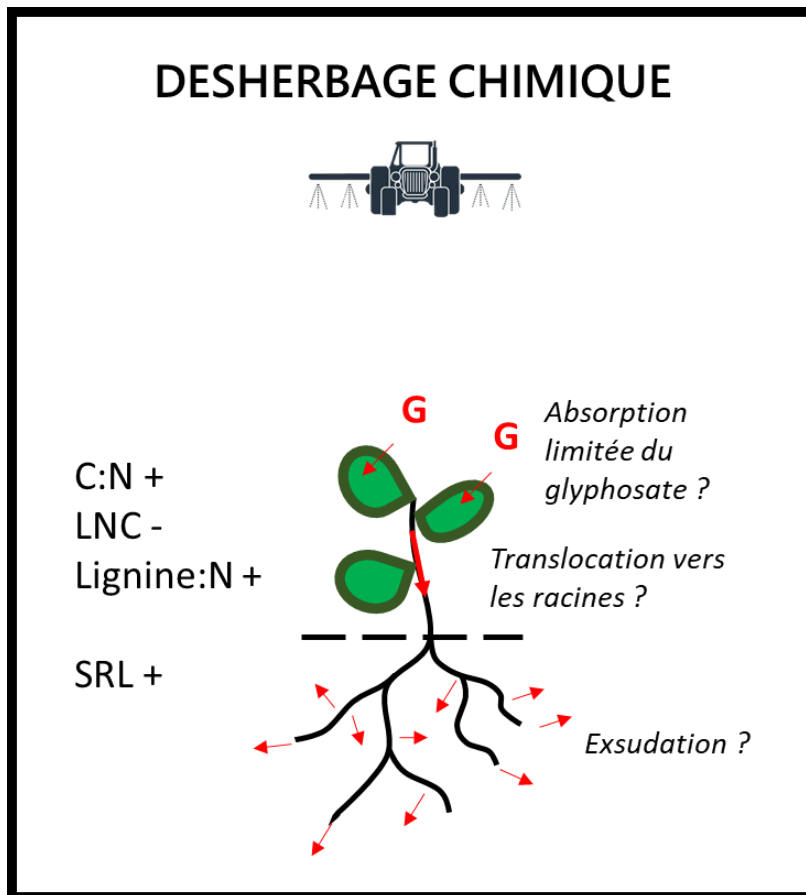


Figure 32 Une interprétation mécaniste possible des propriétés fonctionnelles moyennes d'une adventice d'une communauté issue de parcelles viticoles désherbées chimiquement. Le rapport C:N foliaire élevé peut être associé à la présence d'une cuticule au niveau de la feuille, pouvant diminuer l'absorption du glyphosate. De plus, une des stratégies de résistance au glyphosate peut être de transloquer la molécule vers les racines pour une potentielle exsudation et détoxification. Ce mécanisme a notamment été démontré chez *Poa annua*, très abondante dans les communautés contrôlées par les herbicides, mais l'exsudation n'a pas encore été prouvée.

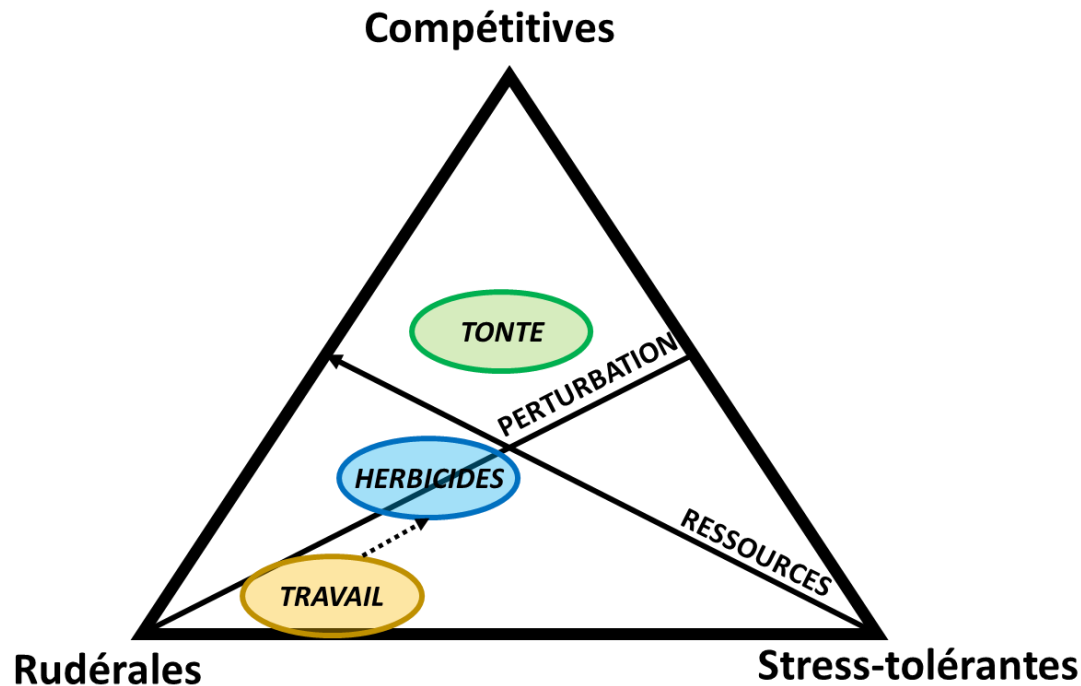


Figure 33 Proposition de repositionnement schématique conceptuel des pratiques de gestion des adventices, les herbicides étant à présent considérés comme des stress.

## 1.5. Le triangle CSR de Grime, adapté aux agroécosystèmes ?

A l'origine, le triangle de Grime est issu de la mesure de trois traits sur des espèces prairiales de Sheffield (hauteur maximale de la canopée, capacité d'élongation latérale et taux de croissance relatif) (Grime, 1974). Dans la thèse, nous avons utilisé un algorithme élaboré par Pierce et al. (2017) basé sur la mesure de trois autres traits: l'aire foliaire, la teneur en matière sèche foliaire et l'aire spécifique foliaire. La validité de cet algorithme a été vérifiée pour des espèces issues de milieux naturels ou semi-naturels (prairies), dans des contextes de perturbations « naturelles » (éboulis en montagne). Le triangle de Grime a donc été théorisé et validé dans les écosystèmes naturels. Mais qu'en est-il pour les agroécosystèmes agricoles ? Pour les agroécosystèmes annuels, Mahaut et al. (2020) proposent de découpler l'axe de ressources de Grime en deux axes: un axe de ressources aériennes et un axe de ressources souterraines. Les auteurs et autrices de cette étude critiquent le fait que le triangle ait été construit sur la description des habitats où se trouvent les espèces (par



exemple des habitats très perturbés et riches en ressources pour les agroécosystèmes annuels) et non pas, sur le niveau de ressources et de perturbations perçues par les espèces y habitant (par exemple, peu de ressources lumineuses pour les adventices des agroécosystèmes annuels, densément semés). Mahaut et al. (2020) transforment le triangle de Grime en cube en plaçant les adventices des agroécosystèmes annuels dans les milieux perturbés, à ressources souterraines élevées (*e.g.* sols fertilisés), mais ayant des ressources aériennes faibles (*e.g.* faible disponibilité en lumière) (Figure 34). Les agroécosystèmes viticoles méditerranéens sont plutôt limités en ressources souterraines (sols secs et peu fertiles) tandis que les ressources aériennes sont élevées (faible densité de plantes cultivées par rapport aux agroécosystèmes annuels et disponibilité de lumière élevée).

**Dans la thèse, nous avons démontré que les propriétés fonctionnelles des adventices répondent significativement aux pratiques de gestion et aux conditions pédoclimatiques et que cette réponse dépendait de l'échelle spatiale considérée. Les propriétés fonctionnelles des communautés adventices contrôlées par le désherbage chimique convergent vers une stratégie stress-tolérante de conservation de ressources foliaires tandis que les communautés issues de parcelles viticoles travaillées sont caractérisées par des stratégies plus rudérales, à plus acquiesitives en ressources et diverses d'un point de vue fonctionnel. Les communautés adventices issues de parcelles viticoles tondues sont également caractérisées par des stratégies foliaires plutôt acquiesitives, à stratégie compétitive.**

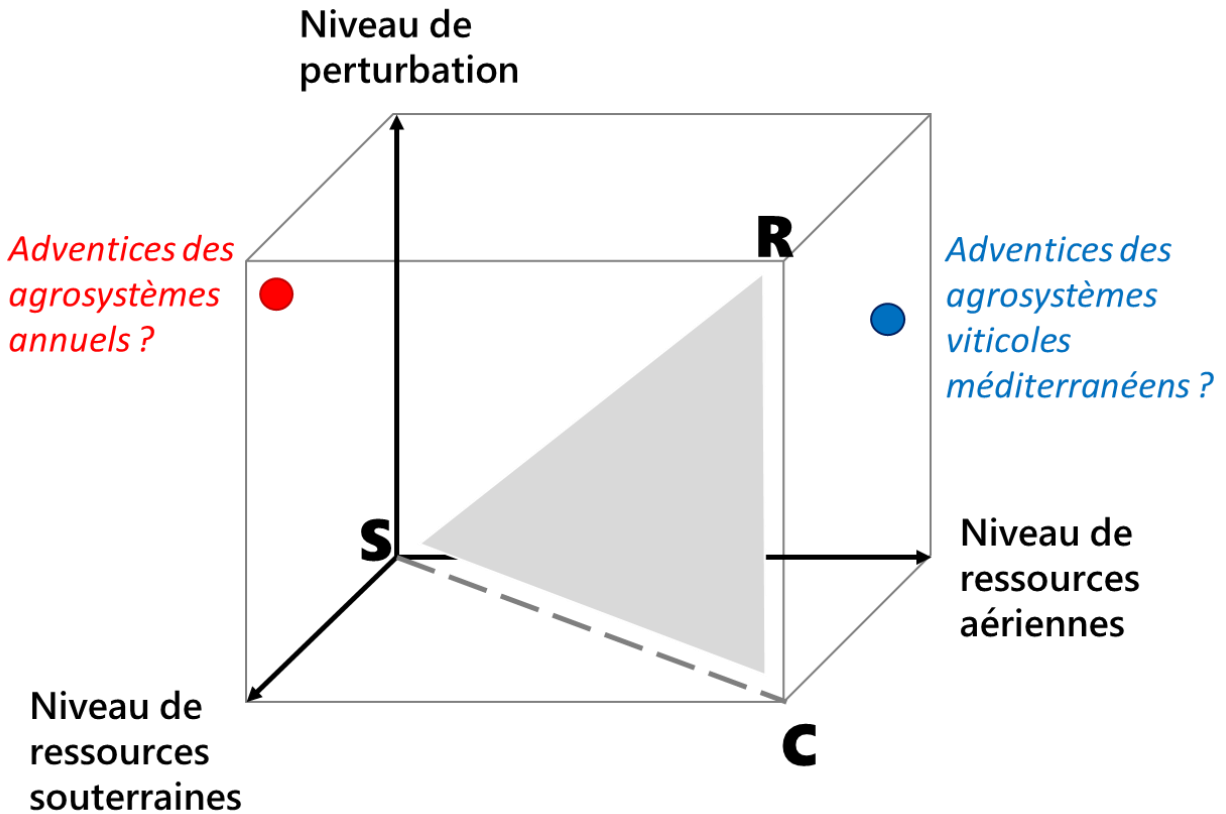


Figure 34 Le cube de Mahaut et al. (2020), largement inspiré d'une des figures de l'article. L'axe de ressources de Grime est découpé en deux axes: les ressources souterraines (e.g. eau, azote) et les ressources aériennes (e.g. lumière). Mahaut et al. (2020) font l'hypothèse que les adventices des agroécosystèmes annuels sont soumis à un régime élevé de perturbations, un niveau élevé de ressources souterraines mais un niveau faible de ressources aériennes (faible disponibilité de lumière dans les agroécosystèmes annuels, densément semés). Nous faisons l'hypothèse que les adventices des agroécosystèmes viticoles méditerranéens sont à l'opposé du carré par rapport aux agroécosystèmes annuels: le niveau de ressources aériennes est élevé (luminosité élevée car les vignes sont moins densément plantées que les cultures annuelles) et le niveau de ressources racinaires est faible (sols méditerranéens peu fertiles).

## 2. Influence des communautés adventices et des pratiques de gestion des couverts sur les processus de recyclage de la matière organique des vignobles

Dans la thèse, nous avons cherché à comprendre comment les communautés adventices influencent les processus de recyclage de la matière organique des vignobles *via* leurs traits d'effets et leurs diversités fonctionnelles au sein des communautés. Premièrement, la décomposition potentielle des adventices a été quantifiée. Deuxièmement, la respiration potentielle (*substrate-induced respiration* ; SIR) a été mesurée comme *proxy* de la biomasse microbienne hétérotrophe<sup>8</sup> du sol. Le potentiel de nitrification (PNEA) et de dénitrification (PDEA) renseigne l'abondance des microorganismes nitrifiants et dénitrifiants des sols et nous avons utilisé des ratios entre potentiels de nitrification et dénitrification et la respiration potentielle (SIR) pour renseigner l'abondance relative des microorganismes nitrifiants (PNEA:SIR) et dénitrifiants (PDEA:SIR) par rapport à la biomasse microbienne hétérotrophe. De plus, nous avons fait le choix d'intégrer les résultats des travaux de la thèse en cours de Léa Genty (UMR ABSys) dans la discussion de cette partie car ces travaux ont été effectués sur une sélection des parcelles de vigne du réseau Maillet. Genty et al., (2022) ont quantifié la digestibilité des communautés adventices, dans la perspective d'une gestion des adventices par pâturage. La digestibilité est définie comme une propriété clé pour évaluer les qualités des plantes à nourrir des ruminants en estimant la digestion de l'animal (Bruinenberg et al., 2002). La digestibilité est corrélée positivement avec la décomposition et est déterminée par les mêmes traits (par exemple, des espèces à teneur d'azote foliaire élevée sont très digestibles et décomposables) (Kazakou et al., 2022).

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<sup>8</sup> Un hétérotrophe est un organisme qui assure sa subsistance en assimilant des substances organiques et des glucides. Il ne peut pas produire ces substances organiques à partir de matière minérale, comme les autotrophes.

## **2.1. Effet des traits moyens des adventices, agrégés à l'échelle de la communauté, sur les processus liés au recyclage de la matière organique dans les vignobles**

Le Tableau 7 synthétise les différentes relations entre les traits d'effet moyens agrégés à l'échelle des communautés adventices et les différents indicateurs de processus mesurés dans la thèse (décomposition potentielle, respiration potentielle *proxy* de la biomasse microbienne hétérotrophe (SIR), ratio entre le potentiel de nitrification et dénitrification et la respiration potentielle) ainsi que le potentiel de digestibilité, mesuré par Genty et al. (2022), sur le même réseau de parcelles de vignes. **Nous avons émis l'hypothèse que les communautés adventices à stratégies d'acquisition de ressources favorisaient un recyclage de la matière organique rapide (décomposition potentielle élevée, abondance de microorganismes nitrifiants, dénitrifiants et biomasse microbienne élevées) au contraire des communautés adventices à stratégies plus conservatrices. Nous ajoutons l'hypothèse posée par Genty et al. (2022): la digestibilité des communautés adventices à stratégie acquisitive est élevée et que celle des communautés adventices conservatives est faible.**

D'après nos résultats, les communautés adventices à teneur en azote foliaire élevée et à C:N foliaire faible sont caractérisées par un potentiel de décomposition (chapitre 4) et de digestibilité élevés (Genty et al., 2022) (Tableau 7), en accord avec les résultats démontrés en écosystèmes naturels et semi-naturels (Bumb et al., 2016; Freschet et al., 2012; Kazakou et al., 2022; Tasset et al., 2019). De plus, les communautés à Lignine:N élevée sont faiblement décomposables (chapitre 4) et celles à teneur en matière sèche foliaire élevée sont faiblement digestibles (Genty et al., 2022). **Ainsi, nous validons notre hypothèse initiale: la décomposition et la digestibilité potentielle des adventices sont élevées pour les communautés adventices à stratégie d'acquisition de ressources.** La variabilité fonctionnelle des valeurs de traits au sein des communautés (LDMC, LN, C:N et Lignine:N foliaires, cellulose, hemicellulose) n'a pas influencé la décomposition potentielle (chapitre 4), contrairement aux résultats des études sur les espèces des écosystèmes naturels (García-Palacios et al., 2017; Plazas-Jiménez and Cianciaruso, 2021). Ainsi, les espèces les plus

abondantes au sein des communautés adventices sont celles qui déterminent la décomposition de l'ensemble de la communauté (« hypothèse de dominance ») tandis que la variabilité de stratégie des adventices au sein des communautés n'est pas significativement reliée à la décomposition potentielle (« hypothèse de complémentarité »).

Les communautés adventices à SRL élevé sont associées à une abondance élevée de microorganismes nitrifiants (PNEA:SIR, chapitre 5) au contraire des résultats de Cantarel et al. (2015), à l'échelle spécifique sur des herbacées pérennes. Ces résultats contradictoires peuvent être dus à la différence d'échelle d'étude (espèce vs communautés) et à la domination des annuelles dans les communautés adventices observées pendant la thèse, qui occupent une place distincte de celle des pérennes dans le « *Root economics spectrum* » (Roumet et al., 2016). Les autres indicateurs de potentiels microbiens (SIR, PDEA:SIR) ne sont pas significativement reliés aux traits moyens agrégés des communautés adventices des vignobles mais au pH et à la texture du sol (chapitre 5).

**Ainsi, les communautés adventices qui investissent dans des structures foliaires résistantes, à stratégie de conservation de ressources, ont un faible potentiel de décomposition et de digestibilité. Les communautés adventices à potentiel d'exploration racinaire du sol élevé sont associées à une abondance élevée de microorganismes nitrifiants.**

Tableau 7 Relations entre traits d'effet moyens agrégés et les différents indicateurs de processus mesurés dans la thèse: la décomposition potentielle, la respiration potentielle ou « Substrate-Induced Respiration » (SIR), le ratio entre le potentiel de nitrification et dénitrification et la Substrate-Induced Respiration (PNEA:SIR et PDEA:SIR, respectivement), ainsi que la digestibilité, mesurée sur les mêmes parcelles de vigne, issue des travaux de Genty et al. (2022). Le sens de la relation trait-processus et la significativité des relations est renseignée par la couleur des cellules (voir la section légende en bas du tableau pour plus de précisions).

		Décomposition (Chap 4)	Biomasse microb. (SIR) (chap 5)	PNEA:SIR (chap 5)	PDEA:SIR (chap 5)	Digestibilité Genty et al. (2022)
Traits foliaires	SLA	-				
	LDMC					
	LNC		-	-	-	
	LCC	-	-	-	-	
	C:N foliaire					
	Cellulose		-	-	-	-
	Hemicellulose		-	-	-	-
	Lignine:N		-	-	-	-
Traits racinaires	SRL	-				-
	C:N racinaire	-				-
	Diamètre racinaire	-				-
	RTD	-				-
Trait plante entière	Hauteur	-				-

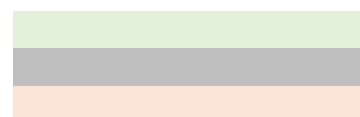
### Légende

Relation positive entre trait moyen agrégé et processus

Relation non significative entre trait moyen agrégé et processus

Relation négative entre trait moyen agrégé et processus

Non testé



-

## **2.2. Effets directs des pratiques de gestion des adventices sur les processus liés au recyclage de la matière organique dans les vignobles**

Le Tableau 8 résume les effets directs d'au moins cinq ans de pratiques de gestion des adventices identiques sur les processus liés au recyclage de la matière organique mesurés dans la thèse et dans l'étude de Genty et al. (2022) ainsi que sur les caractéristiques générales du couvert. **La tonte et le travail du sol favorisent une décomposition potentielle des couverts spontanés plus élevée que le désherbage chimique** (Tableau 8). **De plus, la digestibilité des couverts spontanés est plus élevée lorsque les communautés adventices sont travaillées que lorsqu'elles sont tondues** (Genty et al., 2022). **La biomasse microbienne hétérotrophe du sol est plus élevée sous communautés adventices de parcelles viticoles tondues que sous communautés adventices de parcelles viticoles désherbées chimiquement et travaillées** (Tableau 8). Les pratiques n'ont pas d'effet direct sur les abondances de microorganismes nitrifiants et dénitrifiants. De plus, **les communautés adventices issues de parcelles viticoles travaillées et tondues sont caractérisées par une richesse d'aventices plus élevée et une part plus importante de légumineuses au sein des communautés que les communautés issues de parcelles désherbées**. **La biomasse produite dans les inter-rangs tondues est plus élevée que celle produite dans les inter-rangs désherbés** (Tableau 8).

Sur la base de ces résultats, nous discutons dans la partie suivante des caractéristiques des communautés adventices désirables pour demain, contraintes par les conditions environnementales futures (changement climatique) mais modulables par les pratiques de gestion et l'évolution de la réglementation (abandon du glyphosate ?).

Tableau 8 effets directs des pratiques de gestion des adventices sur les processus liés au recyclage de la matière organique mesurés dans la thèse et dans l'étude de Genty et al. (2022) ainsi que sur les caractéristiques générales des communautés adventices.

		Herbicides	Travail du sol	Tonte
Processus liés au recyclage de la matière organique	Décomposition (Chap 4)			
	Biomasse microb. (SIR) (chap 5)			
	PNEA:SIR (chap 5)			
	PDEA:SIR (chap 5)			
	Digestibilité Genty et al. (2022)	-		
Caractéristiques des communautés adventices	Richesse des communautés			
	Biomasse des communautés			
	% annuelles			
	% légumineuses			
<b>Légende</b>				
Relation positive entre pratique et processus				
Relation non significative entre pratique et processus				
Relation négative entre pratique et processus				
Non testé				

## 2.3. Effets indirects des pratiques de gestion des adventices sur la décomposition potentielle *via* leurs effets sur les propriétés fonctionnelles des communautés adventices des vignobles

Dans le chapitre 4, l'effet indirect d'au moins cinq ans de pratiques de gestion des adventices identiques sur la décomposition potentielle *via* leurs effets sur les propriétés fonctionnelles des communautés adventices a été testé en utilisant une analyse de piste. **Nous avons émis l'hypothèse que les communautés adventices désherbées chimiquement et travaillées sont des communautés à stratégies acquisitives favorisant un recyclage de la matière organique rapide (décomposition potentielle élevée, abondance de microorganismes nitrifiants, dénitrifiants et biomasse microbienne élevées) au contraire des communautés adventices issues de parcelles**



**viticoles tondues.** En désaccord avec notre hypothèse initiale, **nous démontrons dans le chapitre 4 que le désherbage chimique favorise des communautés adventices à stratégie foliaire de conservation des ressources, induisant une décomposition potentielle faible tandis que les communautés adventices issues de parcelles viticoles tondues sont caractérisées par des stratégies foliaires d'acquisition de ressources, induisant une décomposition potentielle élevée** (Figure 35). **Pour le travail du sol, nous validons l'hypothèse initiale.** Par manque d'échantillons<sup>9</sup>, l'effet indirect des pratiques sur les potentiels d'activité microbienne *via* l'effet des pratiques sur les propriétés fonctionnelles des communautés adventices n'a pas pu être testé statistiquement dans le chapitre 5. Cependant, cet effet indirect peut être supposé à partir des relations bivariées testées dans le chapitre 5 à savoir (i) le désherbage chimique favorise les communautés adventices à SRL élevé et (ii) les communautés adventices à SRL élevé sont associées à une abondance de microorganismes nitrifiants élevée dans le sol (Figure 35). **Ainsi, nous émettons l'hypothèse que le désherbage chimique est associé indirectement à des abondances relatives de bactéries nitrifiantes élevées dans le sol *via* des communautés adventices à SRL élevé** (Figure 35). L'utilisation de glyphosate a en effet été associée à une colonisation racinaire faible par les mycorhizes arbusculaires (Druille et al., 2013), induisant une stratégie explorative de ressources à SRL élevé et non collaborative (à diamètre racinaire faible, ne créant pas de conditions adaptées à la colonisation fongique).

## **2.4. Quelles communautés adventices viticoles désirables pour demain et comment les piloter ?**

La thèse s'est basée sur l'analyse de données collectées sur des réseaux de parcelles viticoles en condition de production, existants et (re)construits en début de thèse. En cela, elle s'ancre dans un contexte agronomique réaliste et pédoclimatique varié. En revanche, les pratiques de gestion analysées dans cette thèse sont déjà adoptées par les viticulteurs et viticulteurs et sont relativement

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<sup>9</sup> Le manque d'échantillons est relié au premier confinement de mars 2020, qui a stoppé la campagne de terrain à la moitié de ce qui était prévu

moins « innovantes » que celles testées par certaines études (Boeraeve et al., 2020), comme le désherbage thermique (Mainardis et al., 2020), le pâturage par brebis (Niles et al., 2018) ou, à moindre mesure, l'implantation de couverts végétaux semés (Garcia, 2018). Néanmoins, ce contexte réaliste ainsi que l'approche temporelle du chapitre 3 de la thèse, suscitent l'envie relativement périlleuse d'imaginer les communautés adventices des agroécosystèmes viticoles de demain, contraintes par de nouvelles conditions environnementales (changement climatique), par des pratiques alternatives à l'utilisation d'herbicides (transition agroécologique) et par des nouveaux services écosystémiques attendus (e.g. régulation de la qualité du sol, pollinisation (Blaix et al., 2018; Bretagnolle and Gaba, 2015)).

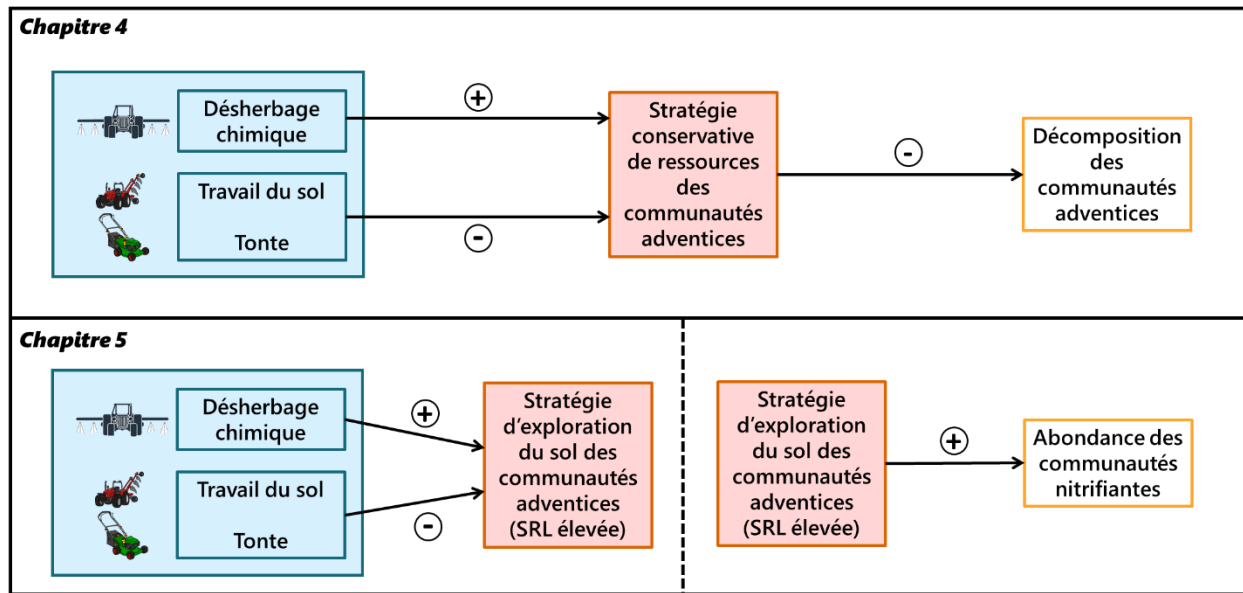


Figure 35 Effet indirect des pratiques de gestion sur la décomposition des communautés adventices et l'abondance des communautés nitrifiantes via leurs effet sur les propriétés fonctionnelles des communautés adventices. Dans le chapitre 4, une analyse de piste a pu établir directement ces effets en cascade tandis que le chapitre 5 n'a pas pu tester directement cet effet, par manque d'échantillons statistiques. Dans ce dernier chapitre, les relations ont été testées deux par deux: pratique -> trait et trait -> processus

### **2.4.1. Des communautés adventices des vignobles adaptées au changement climatique et résilientes**

Le chapitre 3 compare les communautés adventices des années 1980s aux communautés adventices actuelles (2020 et 2021) dans le Montpelliérais (réseau historique « Maillet » de 40 parcelles) en réponse au changement climatique et au changement de pratiques de gestion. En introduction, **nous avons émis les hypothèses suivantes: (i) le changement climatique favorise des communautés adventices stress-tolérantes et (ii) les pratiques de gestion des adventices sont devenues plus intégrées des années 1980s à 2020-2021 et ont sélectionné des communautés adventices moins rudérales.** Nous avons effectivement démontré que les **communautés adventices actuelles sont plus stress-tolérantes que les communautés d'il y a 40 ans, en réponse au changement climatique**, validant notre hypothèse initiale. De plus, nous avons quantifié que **les communautés adventices actuelles sont moins compétitives qu'il y a 40 ans et cette diminution de compétitivité est associée à la complexification des combinaisons des pratiques de gestion** (une à deux pratiques appliquées dans les années 1980s à deux à trois dans les années 2020s). En revanche, les communautés adventices des années 1980s et 2020s ont des scores de rudéralité similaires. Ce résultat fait écho à la synthèse de MacLaren et al. (2020) et leurs propositions d'idéotypes de communautés adventices futures (Figure 36). Selon les auteurs et autrices de cette étude, les communautés adventices actuelles ont des stratégies dont la gamme de variation s'étale de rudérales à compétitives, tandis que les communautés adventices désirées à l'avenir seraient des communautés qui recouvrent l'ensemble de la gamme du triangle de Grime et plus particulièrement des communautés adventices plus stress-tolérantes et moins compétitives (Figure 36). Dès les années 1980s, les communautés adventices du Montpelliérais sont moins compétitives et plus stress-tolérantes que la description schématique des communautés actuelles de MacLaren et al. (2020) (Figure 36). **De plus, nos résultats démontrent bien que les communautés adventices du Montpelliérais ont bien évolué<sup>10</sup> des années 1980s à 2020s vers les idéotypes de communautés adventices proposées par MacLaren et al. (2020).**

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<sup>10</sup> Ici, « évolué » est synonyme de « transformé », « changé » et ne fait pas référence à l'évolution.

A notre connaissance, notre étude est l'une des premières à démontrer une augmentation de richesse (24%) et d'abondance (41%) des adventices au sein d'agroécosystèmes. En cultures annuelles, des tendances significatives opposées ont été démontré entre les années 1970 et 2000 en France (Fried et al., 2016, 2009) ainsi qu'en Europe de 1980 à 2012 (Richner et al., 2015). **Nos résultats suggèrent que les communautés adventices constituent un réservoir de biodiversité résilient, dont le pool d'espèces se renouvelle et s'adapte à des conditions changeantes, qu'elles soient environnementales ou anthropiques.**

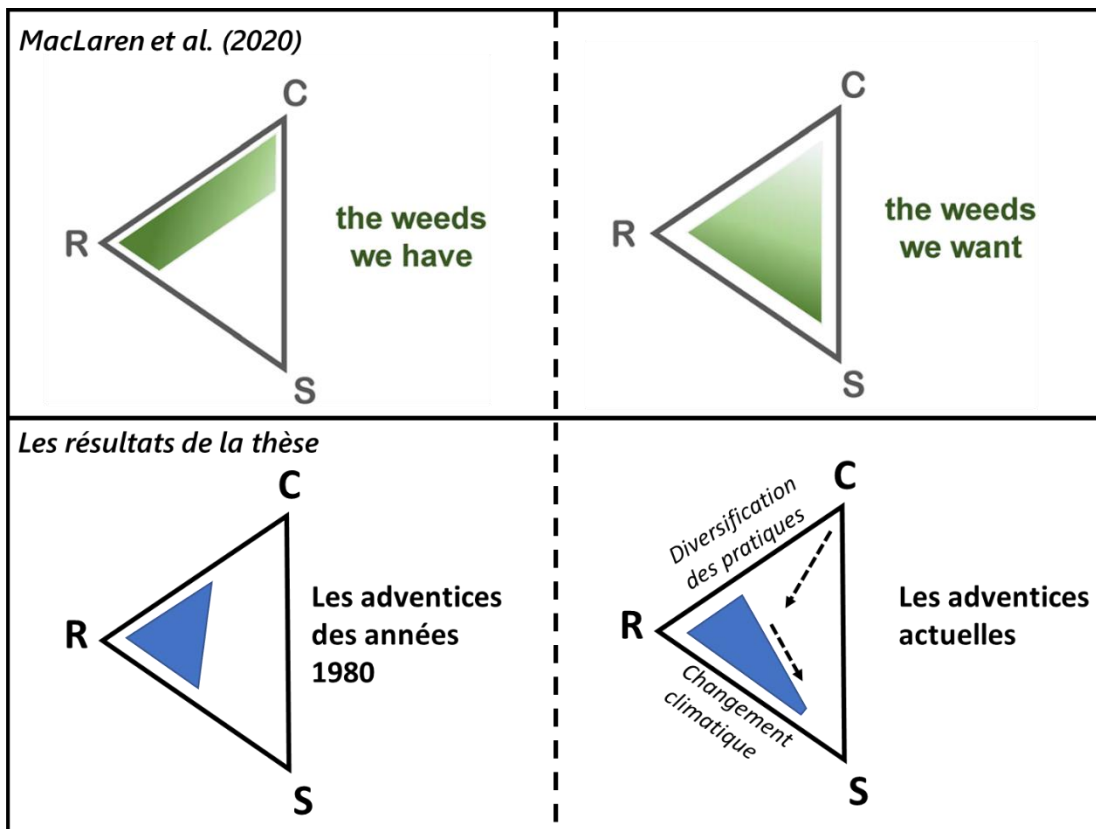


Figure 36 Confrontation des résultats de la thèse (chapitre 3) à la synthèse de MacLaren et al. (2020). Les panneaux du haut présentent la figure issue des travaux de MacLaren et al. (2020) qui illustre schématiquement les communautés adventices actuelles (« the weeds we have ») en haut à gauche et les communautés adventices souhaitables à l'avenir (« the weeds we want ») en haut à droite, au sein du triangle CSR de Grime. Les résultats du chapitre 3 de la thèse sont présentés en bas de la figure. En bas à gauche, l'espace occupé par les communautés adventices des années 1980s du réseau historique Maillet et en bas à droite, le spectre occupé par les mêmes communautés plus de 40 ans après.

#### 2.4.2. Des communautés adventices multifonctionnelles dans les vignobles

La transition agroécologique des agroécosystèmes suppose leurs indépendances progressives vis-à-vis des intrants. En France, l'utilisation du glyphosate a été interdite dans les inter-rangs des parcelles viticoles fin 2020 et la dose sur le rang a été limitée (ANSES, 2020), marquant une dynamique nette de changement de pratiques de l'inter-rang auprès des viticultrices et viticulteurs notre réseau du Montpelliérais. D'après les résultats de la thèse, **la pratique de tonte des adventices semble être la pratique la plus prometteuse pour différentes raisons**. Au bout de cinq ans de cette pratique, la tonte favorise des couverts fortement décomposables (12% plus décomposables que les autres modes de gestion, chapitre 4), à biomasse élevée (47% de biomasse produite en plus par rapport aux autres modes de gestion, chapitre 5), à quantité d'azote contenue dans la biomasse élevée (46% en plus, chapitre 4) ainsi qu'à proportion élevée de légumineuses dans le couvert (33% en moyenne, chapitre 5). La tonte est également associée à une biomasse microbienne hétérotrophe environ deux fois plus élevée que dans les sols des autres modes de gestion (chapitre 5). De plus, c'est la pratique qui promet la plus grande diversité d'adventices au sein de la communauté (deux fois plus d'espèces que dans les autres modes de gestion) (chapitre 5). **Ainsi, la tonte représente à la fois une pratique de gestion des adventices avec la vigne, limitant leurs compétitions lorsque les besoins hydriques et azotés de la vigne sont élevés, mais aussi une pratique d'amendement, restituant une biomasse élevée à forte teneur en azote et un mulch à fort potentiel de décomposition, favorisant une biomasse microbienne du sol élevée**. D'un point de vue plus pratique, la tonte ne nécessite pas d'équipements particuliers supplémentaires (Gaviglio, 2007), est peu coûteuse en énergie (une réduction de 26% d'utilisation de carburant a été quantifiée par rapport au travail du sol (Sanford and Go, 2022)) et peut favoriser d'autres fonctions comme la pollinisation (Johansen et al., 2019). Cependant, la tonte est plus coûteuse financièrement car elle nécessite plus de temps de main d'œuvre (Pergher et al., 2020). Pour implémenter plus largement cette pratique, des aides financières incitatives sont nécessaires pour accompagner les viticultrices et les viticulteurs dans leurs transitions (Gage and Schwartz-Lazaro, 2019).

La biomasse adventice favorisée par la tonte est moins digestible que la biomasse associée au travail du sol, mais les valeurs de digestibilité quantifiées par Genty et al. (2022) sont acceptables

pour du bétail (> 60%) (Hoveland et al., 1986). Les résultats de cette étude suggèrent que la pratique de pâturage des adventices, qui se développent dans les vignobles et notamment au sein de notre réseau dans le Montpelliérais, sont prometteuses (Lazcano et al., 2022; Niles et al., 2018).

### **3. Perspectives de recherche**

#### **3.1. Étudier le ‘dessous’ des adventices pour reconquérir la qualité du sol des agroécosystèmes viticoles: quelles stratégies racinaires des adventices et quelle influence sur les processus du sol ?**

A notre connaissance, le chapitre 5 constitue la deuxième étude qui explore les traits racinaires chez les adventices des agroécosystèmes viticoles (voir Garcia et al., 2019 pour la première). Dans ce chapitre, nous démontrons que les traits racinaires expliquent à eux seuls le premier axe de variation d’une analyse multivariée caractérisant d’un point de vue fonctionnel les communautés adventices, comprenant un ratio équilibré de traits aériens et souterrains. Ces résultats suscitent l’envie d’explorer cette variabilité fonctionnelle souterraine élevée des adventices, d’en comprendre l’origine et l’influence positive ou négative sur les processus des agroécosystèmes.

Par exemple, est-ce que les traits aériens et racinaires des adventices covarient ? Dans le chapitre 5, nous démontrons que les traits chimiques (C:N foliaire et racinaire) covarient mais que les autres traits ne covarient pas (SLA, LDMC, hauteur pour les traits aériens et SRL, diamètre et RTD pour les traits racinaires). Est-ce que cette indépendance aérienne et racinaire est liée au mécanisme de destruction des pratiques de gestion ? Par exemple, Erktan et al. (2018) ont démontré que la tonte décorrèle les traits aériens et racinaires à l’échelle de la communauté car elle induit un plus faible investissement dans les traits aériens tandis que l’investissement dans les traits racinaires demeurent inchangés. Est-ce que la disponibilité de ressources aériennes et souterraines contrastées

dans les agrosystèmes viticoles méditerranéens découple également ces covariations (disponibilité lumineuse élevée, faible fertilité des sols, cf paragraphe 1.5) ?

De nombreuses fonctions écosystémiques du sol sont reliées aux traits racinaires (Bardgett et al., 2014; Freschet et al., 2021): par exemple, le recyclage du carbone et du phosphore ou la capacité des sols à retenir l'eau. Certains traits racinaires, plus coûteux en termes de mesure mais plus proche des mécanismes (« *hard traits* » *sensus* Violle et al. (2007)) pourraient être particulièrement intéressants à quantifier pour les adventices: par exemple, est-ce que les adventices exsudent ? La biomasse racinaire des communautés adventices étant faible dans les agrosystèmes viticoles, est-ce que la quantité et qualité des exsudats influencent néanmoins les processus du sol ?

### **3.2. Définir la carte d'identité fonctionnelle des adventices des systèmes de culture à base de pérennes pour mieux explorer leurs fonctionnalités**

En France, Bourgeois et al. (2019) ont défini l'identité fonctionnelle des adventices des cultures annuelles par rapport aux espèces herbacées de milieux ouverts. Les auteurs et autrices de cette étude ont démontré que les adventices sont principalement thérophytes, ont des SLA élevées, fleurissent précocement et sur une longue période et ont une grande affinité pour les sols riches en nutriments, ensoleillés et sec. Mais qu'en est-il pour les adventices des agroécosystèmes viticoles et notamment des agroécosystèmes méditerranéens ? Et quelle implication pour leurs multifonctionnalités ? Les conditions environnementales (sols pauvres pour les vignobles méditerranéens et sols fertiles pour les cultures annuelles), la densité de plantation (faible pour les vignobles et élevée pour les cultures annuelles), les pratiques de fertilisation (faible apport pour les vignobles et apport élevé pour les cultures annuelles) et les pratiques de gestion du sol (travaux du sol plutôt profonds pour les cultures annuelles versus grattage superficiel des sols dans le cas des agroécosystèmes viticoles) suggèrent une identité fonctionnelle distincte entre les adventices des cultures annuelles et les adventices des cultures pérennes (cf paragraphe 1.5 de la discussion

générale). Au-delà des valeurs de traits moyens, les communautés adventices des agroécosystèmes viticoles méditerranéens sont peut-être également caractérisées par une variabilité fonctionnelle élevée. Cette diversité fonctionnelle, illustrée par exemple par la localisation étendue des adventices dans le triangle de Grime (Figure 26) ou par des dessins d'écologues (Figure 37), représente une réserve de diversité précieuse pour assurer la résilience des agroécosystèmes et leurs indépendances aux intrants. Par ailleurs, ce qui caractérise les communautés adventices en général, est peut-être plus simplement cette variabilité fonctionnelle, qu'une série de valeurs moyennes de trait. La Figure 37 représente onze dessins d'adventices, effectués par des écologues et par des viticulteurs et viticultrices. La diversité des familles biologiques des adventices dessinées est élevée : on reconnaît des poacées (Figure 37F, I, E ? et J?), un coquelicot (Figure 37H), un chardon (Figure 37D), une malvacée (Figure 37B), une brassicacée (Figure 37K) et un chêne qu'on peut effectivement retrouver sous le rang de vigne, sous forme de plantule (Figure 37C).

Quelle est l'implication de cette variabilité fonctionnelle des communautés adventices pour le fonctionnement des agroécosystèmes ? Si certains articles ont intégré la diversité fonctionnelle des communautés adventices comme variable de réponse aux pratiques (*e.g.* (Hall et al., 2020)), peu d'études ont encore intégré des indices de diversité fonctionnelle comme métrique fonctionnelle d'effets. Plus généralement, la plupart des études sur les adventices se sont concentrées à comprendre leurs réponses aux pratiques de gestion tandis qu'encore peu d'études ont testé les liens entre traits d'effets et fonctionnement des agroécosystèmes (Gaba et al., 2017). De plus, l'identification des traits d'effets pertinents et spécifiques à chaque processus étudié au sein des agrosystèmes est essentiel pour tendre vers une meilleure compréhension des mécanismes (Blaix et al., 2018; Martin and Isaac, 2015).



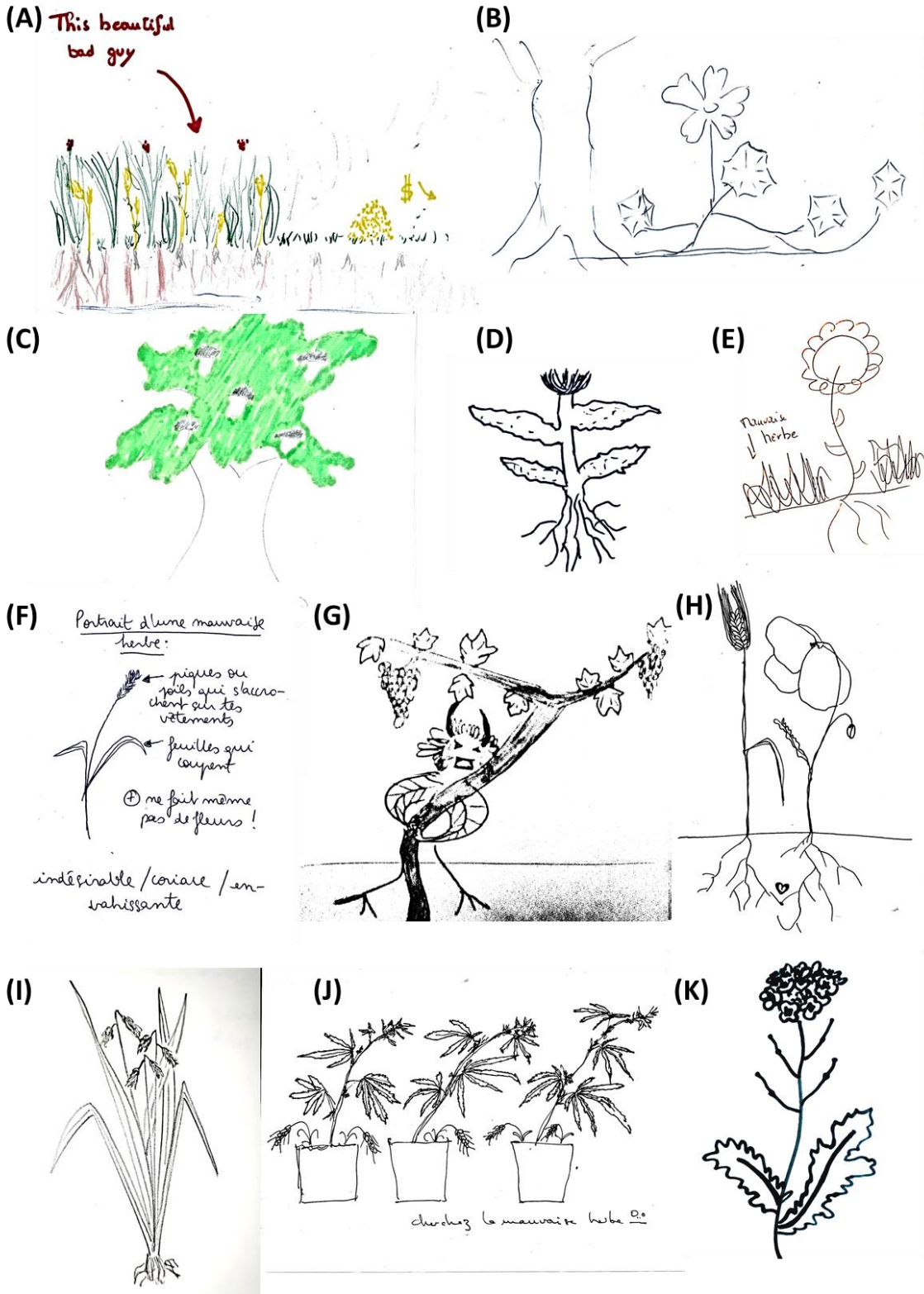


Figure 37 Dessins d'adventices effectués par des écologues en réponse à la commande initiale : « Dessine-moi une mauvaise herbe »

## CONCLUSION DE LA THESE

La thèse a permis de mieux comprendre la réponse des communautés adventices aux pratiques de gestion (désherbage chimique, travail du sol, tonte), à différentes échelles spatiales et dans le temps. Nous avons aussi quantifié le potentiel de décomposition des adventices et leurs effets sur les potentiels d'activité microbienne des sols. **Nous montrons que la tonte est une alternative aux herbicides particulièrement prometteuse car elle favorise des couverts spontanés décomposables, à biomasse et teneur en azote élevées, riches en espèces adventices et associés à une biomasse microbienne élevée.** Cette thèse démontre une certaine forme de résilience des communautés adventices aux changements de pratiques de gestion ainsi que leurs adaptabilités au changement climatique, à l'échelle du pool régional. L'intégration progressive des pratiques de gestion des sols des adventices (moins de désherbage chimique, plus de combinaisons de pratiques), accrue par un contexte réglementaire qui se durcit (ANSES, 2020), modèle des communautés adventices plus riches, plus abondantes et moins compétitives. Cette thèse démontre que la gestion des adventices est un indéniable levier d'action pour gérer les couverts spontanés des agroécosystèmes, transformant les communautés de mauvaises herbes en communautés de plantes de services pour l'aire 'post-herbicide' (Merfield, 2022).



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# ANNEXES



*Veronica agrestis*

Photo de Guillaume Fried (Hérault, mars 2020)



# **Article de vulgarisation 1 – L’approche fonctionnelle appliquée au cas des adventices des vignobles**

Bopp, M.-C., Fried, G., Metay, A., & Kazakou, E. (2021). L’approche fonctionnelle appliquée au cas des adventices des vignobles. *Revue Des Oenologues*, 191, 22–23.





# L'approche fonctionnelle appliquée au cas des adventices des vignobles

## Mesurer leurs traits pour prédire leurs effets sur le fonctionnement des agrosystèmes viticoles

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### Introduction

L'agroécologie repose sur la réintroduction de la biodiversité au sein des agrosystèmes dans le but de favoriser les interactions biotiques et de fournir des services écosystémiques, c'est-à-dire, les contributions de l'écosystème au bien-être humain. Au sein des parcelles viticoles, les interrangs représentent des espaces disponibles pour augmenter la biodiversité floristique. Les adventices ont longtemps été considérées comme des « mauvaises herbes » pour leurs impacts négatifs sur la quantité et la qualité du rendement viticole (**encadré 1**). L'émergence de l'agroécologie questionne leur utilité au sein des vignes et l'obligation réglementaire de réduction d'intrants contraint les agriculteurs à adapter leurs gestions des adventices. Depuis les années 2000, de nouvelles pratiques de gestion du sol sont mises en place permettant une présence plus longue des adventices dans l'interrang : enherbement permanent naturel ou semé, géré par des tontes régulières ; enherbement naturel hivernal détruit au printemps par le travail du sol... Pour étudier l'effet de ces nouvelles pratiques de gestion du sol sur les adventices, une approche fondée sur une définition plus « fonctionnelle » de la biodiversité peut être utilisée. Elle s'appuie sur la mesure de « traits », soit des caractéristiques morphologiques, physiologiques ou phénologiques mesurées

■ **Encadré 1 : Des « mauvaises herbes » aux « adventices » : un changement de terminologie qui traduit le l'évolution de la perception de la flore des milieux cultivés par l'homme.**

« *Qu'est-ce donc qu'une mauvaise herbe, sinon une plante dont on n'a pas encore découvert les vertus ?* »  
R.W. Emerson, fin du XIX<sup>e</sup> siècle

Les mauvaises herbes sont « des plantes indésirables là où on les trouve ». En agriculture, la nuisibilité se définit par rapport à un objectif de production : stabilité du rendement, confort et qualité de la vendange. En ce sens, les mauvaises herbes ou « herbes folles » peuvent contraindre la réalisation de ces objectifs, si elles sont mal maîtrisées, en entrant en concurrence avec la vigne pour l'eau et les éléments minéraux ou en gênant les chantiers de récolte.

Ces dernières années, l'émergence de l'agroécologie a contribué à un changement de perception sur les mauvaises herbes dans le milieu agricole. Les mauvaises herbes constituent une composante majeure de la biodiversité dans le milieu cultivé et participent au fonctionnement de l'agrosystème. Elles peuvent ainsi constituer de « bonnes herbes », utiles à l'agriculteur-ice, en fournissant des services écosystémiques : attraction des auxiliaires de culture, réduction de l'érosion des sols, valorisation de l'aspect esthétique des parcelles lors de la floraison, etc.

Le terme « adventice » refait surface. Ce mot provient du latin *adventicius* qui signifie « venant du dehors » et est défini comme « une plante se développant dans une culture sans y avoir été volontairement introduite par l'homme ». Ce terme est privilégié en recherche agronomique car jugé « plus neutre » et sera donc employé dans cet article. Ce changement de terminologie illustre le changement de perception de la flore des milieux cultivés et le regain d'intérêt dont elle fait l'objet dans le contexte de l'agroécologie.

sur les adventices (Violle et al., 2007). Ces traits sont dits « fonctionnels » (p. ex., teneur en matière sèche des feuilles) car ils sont associés à des fonctions spécifiques à l'échelle de la plante et des communautés (p. ex., décomposition). Les adventices peuvent être filtrées par les pratiques de destruction (mécanique, chimique) et de régulation (tonte), favorisant des communautés adventices aux valeurs de traits adaptées. Ces valeurs de traits, en particulier celles des espèces dominantes, peuvent avoir une influence sur différents processus écologiques (minéralisation des nutriments, séquestration de carbone dans le sol...). Évaluer la biodiversité fonctionnelle permettrait ainsi de quantifier la contribution des adventices à la fourniture potentielle de services écosystémiques (nutrition minérale de la vigne, régulation du climat...).

Cet article vise à présenter l'application de l'approche fonctionnelle aux adventices des vignes.

### L'impact spectaculaire des changements de pratiques de gestion du sol sur la flore adventice dans les vignes

Les pratiques de gestion du sol ont rapidement évolué depuis les années 1960. Les changements de pratiques ont mis en évidence leurs impacts parfois spectaculaires sur la composition en adventices dans les parcelles de vigne.

Au début du XX<sup>e</sup> siècle, la technique du chassage-déchaussage est largement répandue en viticulture. Elle consiste à former une butte de terre au niveau des ceps de vigne pour les protéger du gel en hiver (« buttage »). La terre de la butte est dégagée au printemps (« débutage ») par les charrues vigneronnes. L'interrang est travaillé superficiellement pour éliminer les adventices.

Dans les années 1960-1970, la mise sur le marché d'herbicides, efficaces et pratiques à utiliser, marque une première rupture dans la gestion des adventices. Le désherbage chimique sur le rang remplace peu à peu la pratique du chassage-déchaussage. Le travail superficiel du sol dans l'interrang est maintenu dans certains cas tandis que le désherbage en plein est pratiqué dans d'autres cas en abandonnant tout travail du sol. L'émergence de la pratique de désherbage est à l'origine de changements majeurs dans la composition et la richesse des communautés d'adventices entre les années 1970 et 1990. Les malherbologues parlent même d'une « inversion de

la flore » (Maillet, 1992). Dans une étude menée sur des vignes du Montpellièrais en début d'été, des adventices telles que l'ivraie raide (*Lolium rigidum*) ou la vergerette de Sumatra (*Erigeron sumatrensis*) se répandent dans les parcelles de vignes (figure 1) (Maillet, 1992). Dans cette même étude, d'autres adventices se raréfient comme le panic rude (*Setaria verticillata*) ou le coquelicot (*Papaver rhoeas*). Au début des années 2000, les problèmes liés à la présence de sols « nus » (appauvrissement en matière organique, érosion accrue, portance faible...) révèlent la nécessité du maintien d'un couvert hivernal dans les interrangs et conduisent à abandonner le désherbage d'automne. Par ailleurs, la découverte de résidus persistants issus de substances actives de pesticides dans les cours d'eau français, contribue à la diminution de leur utilisation. Une grande diversité de pratiques de gestion de sol a émergé suite à la diminution des pratiques de désherbage : enherbement naturel hivernal, enherbement semé permanent, etc.

### Une approche fonctionnelle de la biodiversité

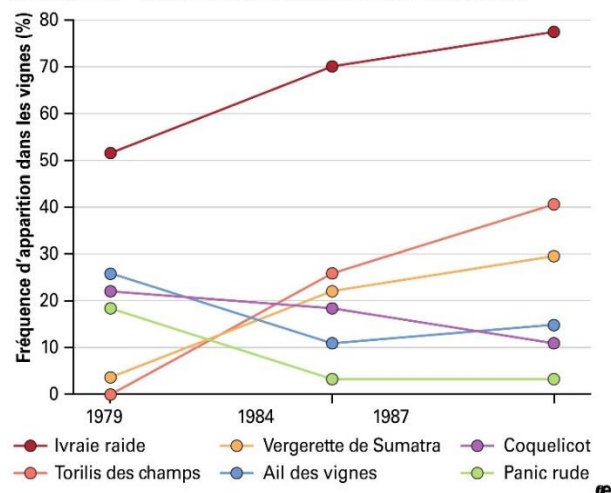
La biodiversité est couramment conceptualisée et mesurée par un nombre d'espèces, de genres et de familles. Environ 900 espèces d'adventices ont été répertoriées dans les vignes françaises par les botanistes soient 75 % des adventices françaises toutes cultures confondues (Maillet, 2006). Si cette facette taxonomique de la diversité par des binômes latins permet de bien décrire la biodiversité des adventices présentes dans les vignes, elle ne permet pas de comprendre le rôle de ces plantes dans le fonctionnement de l'agrosystème. Comment ces 900 espèces contribuent-elles aux processus de fixation d'azote, de réduction de l'érosion, de séquestration de carbone dans le sol ? Pour répondre à ces questions, l'évaluation de la composante « fonctionnelle » de la biodiversité est nécessaire. Complémentaire à l'approche taxonomique, celle-ci tient compte du rôle des espèces dans l'agrosystème. L'approche fonctionnelle se fonde sur la mesure de caractéristiques mesurables à l'échelle de la plante : les traits fonctionnels (Violle et al., 2007). Par exemple, le trait fonctionnel de la profondeur d'enracinement d'une plante permet d'évaluer sa capacité à extraire l'eau du sol. Il existe deux types de traits fonctionnels :

- les traits qui permettent de prédire l'impact des adventices sur le fonctionnement de l'agrosystème sont nommés « traits d'effet » (figure 2) ;
- les traits sensibles à l'impact de l'environnement et des activités humaines sont appelés « traits de réponse ».

### Les pratiques de gestion du sol filtrent les traits des adventices

Les chercheurs en écologie des communautés étudient l'adaptation de la flore aux contraintes environnementales. Ces contraintes agissent comme des « filtres » en sélectionnant les espèces ayant des valeurs de traits adaptées. Elles peuvent ainsi se développer dans ce milieu

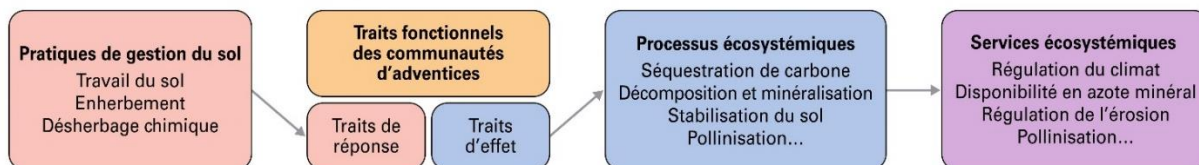
■ **Figure 1 : Changement dans la fréquence de quelques adventices illustrant l'« inversion de flore » observée sur 70 parcelles de vigne du Montpellièrais de 1979 à 1987** (Maillet, 1992). Les inventaires ont été effectués en début d'été.



et enrichir le stock de semences au détriment des autres espèces. Les filtres environnementaux classiquement étudiés sont les stress liés au manque de ressources (eau, nutriments) et les perturbations (destruction brutale des plantes). Cette « Théorie des filtres environnementaux » peut être appliquée aux filtres d'origine anthropique en parcelles agricoles comme les pratiques culturales mises en place dans les vignobles : ainsi, au même titre que les filtres environnementaux, le travail du sol, le désherbage chimique et la tonte des adventices filtrent les adventices présentes selon leurs valeurs de traits (Kazakou et al., 2018). Au sein d'une même parcelle de vigne, la gestion différente des interrangs (par exemple, un interrang sur deux travaillé et un interrang sur deux tondu) implique des changements de composition visible à l'œil nu (figure 3). De plus, une étude a

récemment montré que la tonte favorisait les espèces ayant des rosettes comme les pâquerettes (Fried et al., 2019). En effet, la position basale des feuilles en rosette évite la destruction de la majeure partie de l'appareil photosynthétique lors de la tonte et permet à la plante de conserver sa vigueur suite à la coupe de la tige. Cette même étude a montré que les travaux du sol superficiel laissent passer les espèces possédant des rhizomes (tige souterraine) comme les chiendents (*Elytrigia* sp.). Dans ce cas, les dents des outils découpent les rhizomes, favorisant ainsi leurs multiplications végétatives et leurs propagations. De plus, le désherbage chimique et le travail du sol favorisent les espèces estivales à germination tardive (avril, mai) car ces pratiques éliminent les espèces hivernales ayant germé à l'automne. Le désherbage chimique favoriserait également les espèces ayant des

■ **Figure 2 : Cadre conceptuel des réponses des adventices aux pratiques de gestion du sol et de leurs effets sur les processus écosystémiques** (adapté de (Kazakou et al., 2016)).



feuilles avec une couche épaisse de cuticule (couche externe lipidique). En effet, l'imperméabilité de la surface de ces feuilles permet de limiter l'absorption des gouttes de la substance active (figure 4).

### Les effets des adventices sur les processus écosystémiques : l'exemple sur le fonctionnement du sol

La présence des adventices modifie le fonctionnement du sol dans les vignes. La mesure des traits d'effet permet de comprendre leurs impacts sur différents processus écosystémiques. Deux exemples de processus sont détaillés dans cette partie.

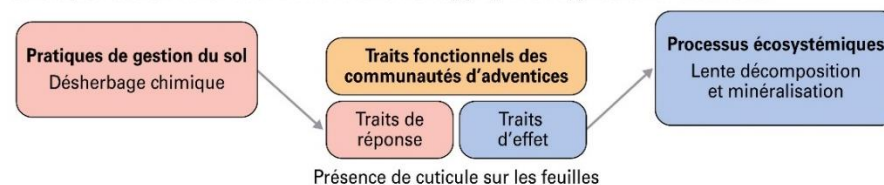
#### Décomposition et minéralisation des adventices

La décomposition et la minéralisation sont les deux processus les plus étudiés dans les approches fonctionnelles. Ces deux processus sont particulièrement déterminants dans un contexte agronomique car ils conditionnent la nutrition minérale de la vigne. En écologie fonctionnelle, les traits des feuilles comme la teneur en matière sèche (rapport de la masse sèche sur la masse fraîche des feuilles) ou la surface foliaire spécifique sont particulièrement mesurés car ils représentent bien les caractéristiques de la plante entière. De nombreuses études ont montré que les feuilles à teneur en matière sèche élevée se décomposaient plus lentement. Dans les parcelles de vigne, la tonte de l'enherbement génère une litière laissée sur place après l'intervention. L'étude des traits de cette litière est un moyen d'estimer la vitesse de décomposition et le retour de nutriments au sol, potentiellement disponibles pour la nutrition minérale de la vigne (figure 4).

■ **Figure 3 : Exemple d'une parcelle de vigne près de Campagne (34) avec une gestion différenciée des interrangs** (un sur deux est travaillé et les autres interrangs sont tondus). **Le changement de composition floristique induit par ces différentes pratiques est visible à l'œil nu** : un interrang sur deux, les fausses roquettes (*Diplotaxis erucoides*), bien visibles avec leurs fleurs blanches sont favorisées par le travail du sol.



■ **Figure 4 : Exemple de la pratique de désherbage chimique et de la compréhension des conséquences sur le fonctionnement du sol en appliquant l'approche fonctionnelle.**



#### Séquestration de carbone dans le sol

La séquestration de carbone dans le sol est un processus majeur déterminant la fourniture du service écosystémique de la régulation du climat. En effet, le carbone atmosphérique est capté par les adventices via la photosynthèse. L'humification d'une partie de la matière organique des adventices sénescentes augmente le stockage de carbone dans le sol. Ainsi, les traits reliés à la décomposition cités dans le paragraphe précédent sont également reliés au flux de carbone dans le sol. De plus, les racines des adventices sécrètent des composés carbonés particulièrement stables dans le sol (ce phénomène est appelé l'exsudation racinaire). Plus ces sécrétions sont faites en profondeur, plus le carbone sécrété sera minéralisé lentement

et plus stabilisé dans le sol. Ainsi, des adventices ayant de longues racines profondes permettent une meilleure séquestration de carbone (Birouste, 2014).

#### Conclusion

L'approche fonctionnelle permet de mieux comprendre les réponses des adventices aux pratiques de gestion du sol et leurs effets sur le fonctionnement de l'agrosystème viticole. Les traits classiquement utilisés ont l'avantage d'être particulièrement faciles à mesurer et ce, à moindre coût. Cette approche présente l'avantage d'être applicable à l'échelle des communautés, une échelle particulièrement adaptée au contexte agronomique. Peu d'études l'ont encore appliquée aux parcelles de vignes et les recherches actuelles se situent encore en amont d'une réelle application. Pourtant, l'approche fonctionnelle pourrait permettre de prédire l'impact de nouvelles pratiques culturales agroécologiques sur les processus de l'agrosystème et la fourniture de services grâce à la mesure simultanée de traits d'effet et de réponse.

Une seconde perspective, qui pourrait être envisagée, serait la conception d'idéotypes d'enherbements semés avec des traits adaptés reliés à certains services spécifiques répondant aux besoins des agriculteurs-rices. ■

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**Article de vulgarisation 2 – Impact des pratiques de gestion des adventices sur la flore des vignes de trois grandes régions viticoles françaises**



# Impact des pratiques de gestion des adventices sur la flore des vignes de trois grandes régions viticoles françaises

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Les adventices représentent une part importante de la biodiversité présente dans les vignes. Environ 900 espèces d'adventices ont été répertoriées dans les vignes françaises par les botanistes soient 75 % des adventices françaises toutes cultures confondues. Depuis les années 2000, de nouvelles pratiques de gestion tolérant davantage la présence des adventices dans l'inter-rang sont mises en place : enherbement permanent naturel ou semé, géré par des tontes régulières ; enherbement naturel hivernal détruit au printemps par travail du sol... Pour étudier l'effet de ces nouvelles pratiques sur les adventices et leurs stratégies d'adaptation, l'approche fonctionnelle, issue de l'écologie comparative, peut être appliquée au système viticole. Cette approche s'appuie sur la mesure de « traits », soit des caractéristiques morphologiques, physiologiques ou phénologiques mesurées sur les plantes. Les adventices peuvent être favorisées par les pratiques de destruction (mécanique,

chimique) et de régulation (tonte). Étudier les valeurs de traits des adventices permet de mieux comprendre comment la flore s'adapte aux pratiques de gestion. De plus, les traits, particulièrement ceux des espèces dominantes, peuvent en retour avoir une influence sur différents processus écologiques (minéralisation des nutriments, séquestration de carbone dans le sol...). Évaluer la biodiversité fonctionnelle permet donc de mieux appréhender la réponse des adventices aux pratiques de gestion du sol d'une part et de quantifier la contribution des adventices à la fourniture potentielle de services écosystémiques (nutrition minérale de la vigne, régulation du climat...) d'autre part. **Cet article vise à démontrer, via un exemple concret, comment l'approche fonctionnelle permet de mieux comprendre la réponse des adventices aux pratiques de gestion viticoles.** Pour cela, nous avons utilisé une grande base de données, caractérisant la biodiversité végétale associée au milieu viticole, issue

du réseau « Biovigilance Flore », mis en place par le Service de la Protection des Végétaux. Deux cent soixante-dix relevés floristiques ont été effectués dans 45 parcelles de 3 régions viticoles françaises (Champagne, Languedoc-Roussillon et Vallée du Rhône) de 2006 à 2012 sur plusieurs saisons (fin d'hiver, début d'été et automne) (**Figure 1**).

## 1 - L'adaptation des plantes aux niveaux de ressources et de perturbations de leurs milieux selon les stratégies de Grime :

En 1973, Grime caractérise 3 grandes stratégies mises en place par les plantes pour s'adapter à leur milieu. Les espèces peuvent être (i) compétitives (en particulier dans les milieux riches en ressources, comme les prairies fertilisées), (ii) tolérantes aux perturbations (par exemple, un travail du sol, un désherbage chimique) ou (iii) tolérantes aux stress (par exemple, un stress hydrique). Plus récemment, des



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études ont montré que ces stratégies pouvaient être prédites à partir des valeurs de 3 traits foliaires (**Table 1**).

Premièrement, l'aire foliaire renseigne de la capacité d'une plante à intercepter la lumière et par conséquent, de sa compétitivité pour cette ressource (**Table 1**). Deuxièmement, l'aire spécifique foliaire, qui est le ratio entre la surface foliaire et la masse sèche foliaire, est un indicateur pertinent de la surface de feuille allouée à la photosynthèse par unité de biomasse sèche investie. Ainsi, les plantes à surface foliaire spécifique élevée maximisent la photosynthèse pour un coût de construction de la feuille réduit ; elles ont ainsi une stratégie d'acquisition sur le court terme et ont une plus grande tolérance aux milieux perturbés et incertains où des pratiques de gestion peuvent détruire la biomasse végétale (par exemple, le travail du sol ou le désherbage chimique). Enfin, la teneur en matière sèche foliaire est un bon indicateur de l'investissement d'une plante dans la construction de ses feuilles. En effet,

plus une feuille a une teneur en matière sèche élevée, plus les tissus cellulaires de la feuille sont denses, plus la feuille a été « coûteuse » à construire pour la plante par unité de biomasse sèche. Cet investissement dans la construction de la feuille peut être fait pour s'adapter à un milieu stressant (**Table 1**). Par exemple, les plantes des milieux avec une disponibilité en eau réduite ont des feuilles denses à teneur en matière sèche élevée qui limitent la perte en eau via l'évapotranspiration.

## 2 - Les stratégies des adventices de Champagne, du Rhône et du Languedoc

En utilisant les relevés floristiques de chaque région et les valeurs de traits de chaque espèce, issues de bases de données, la compétitivité, la tolérance aux perturbations et aux stress des plantes de chaque région ont été estimées (**Figure 2**).

Les analyses ont montré que les communautés d'adventices du Languedoc-Roussillon présentent des caractéristiques morphologiques associées à une plus grande tolérance aux stress que les communautés de la Vallée du Rhône. En effet, 19 % des communautés d'adventices étaient classées dans la catégorie des tolérantes au stress selon leurs valeurs de traits en Languedoc-Roussillon contre 15 % dans la Vallée du Rhône (**Figure 2**).

Le climat chaud et sec Méditerranéen du Languedoc-Roussillon peut expliquer les adaptations morphologiques des adventices au stress hydrique comme une teneur en matière sèche des feuilles plus élevée. En effet, les cellules des feuilles de plantes en stress hydrique sont plus petites et forment des couches denses, ce qui se traduit par une fraction plus faible d'espace d'air dans la feuille. Ces feuilles sont plus rigides et sont moins sujettes au flétrissement en conditions sèches. Ainsi, le rapport entre masse sèche et masse fraîche plus élevé peut traduire l'adaptation des plantes languedociennes à un stress

hydrique plus intense dans cette région par rapport à la vallée du Rhône.

Les communautés de la Vallée du Rhône sont caractérisées par une plus grande tolérance aux perturbations que les communautés languedociennes (par exemple les travaux du sol ou le désherbage chimique), tandis que les communautés champenoises ne sont pas significativement différentes des deux autres régions. En effet, 52 % des communautés d'adventices rhônaises étaient classées dans la catégorie des tolérantes aux perturbations selon leurs valeurs de traits contre 48 % dans le Languedoc-Roussillon (Figure 2).

Le désherbage chimique des inter-rangs est plus fréquent sur les parcelles de la Vallée du Rhône (45 % des parcelles concernées) que sur les parcelles languedociennes (26 % des parcelles). En Languedoc, les inter-rangs sont surtout travaillés. Si on fait l'hypothèse que le désherbage chimique est une plus grande perturbation que le travail du sol, l'utilisation d'herbicides plus marquée dans la Vallée du Rhône pourrait expliquer la plus grande tolérance aux perturbations de ses communautés d'adventices. Enfin, les communautés des différentes régions ne se différencient pas par rapport à leurs compétitivités.

### 3 - Les stratégies d'adaptation des adventices à la tonte, au travail du sol et au désherbage chimique : l'exemple du Languedoc-Roussillon

Les régions viticoles de l'étude étant caractérisées par des pédoclimats et des pratiques différentes, nous avons exploré le lien entre pratiques et certains traits pour chacune des régions pour mieux comprendre les stratégies d'adaptation des adventices. Ici, nous

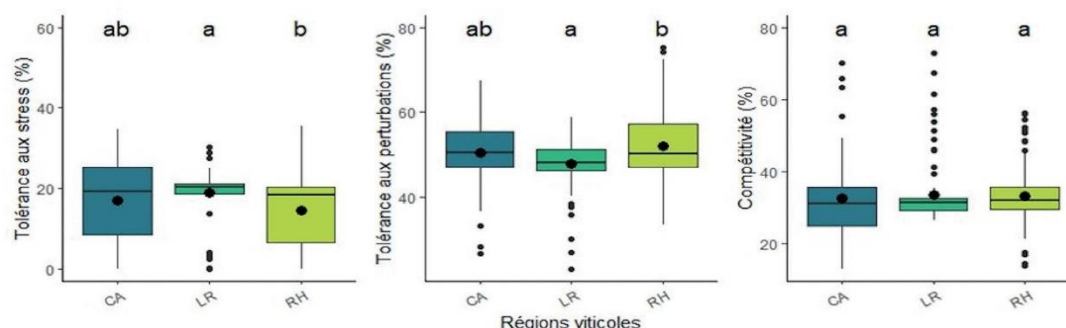
Traits mesurés	Unité	Calcul	Signification	Lien avec les stratégies des plantes
Aire foliaire	mm <sup>2</sup>	-	Capacité d'une plante à intercepter la lumière	<b>Compétitivité</b> Plus une plante a une aire foliaire élevée, plus elle est compétitive pour intercepter la lumière
Aire spécifique foliaire	mm <sup>2</sup> .mg <sup>-1</sup>	= aire foliaire / masse sèche foliaire	Investissement en matière sèche dans la construction de la surface allouée à la photosynthèse	<b>Tolérance aux perturbations</b> Plus une plante à une aire spécifique foliaire élevée, plus elle maximise la surface photosynthétique tout en minimisant les coûts de construction de la feuille en masse de matière sèche.
Teneur en matière sèche foliaire	mg.g <sup>-1</sup>	= masse sèche foliaire / masse fraîche foliaire	Investissement dans la construction de la feuille en matière sèche	<b>Tolérance au stress</b> Plus une plante à une teneur en matière sèche, plus elle investit dans la construction de la feuille pour s'adapter aux stress de son milieu (par exemple, investissement dans une cuticule pour limiter les pertes en eau en stress hydrique)

**Table 1 :** Les caractéristiques mesurées sur les adventices et les interprétations de leurs valeurs en termes de stratégies écologiques des adventices.

présentons les résultats dans le Languedoc-Roussillon. Cette région est caractérisée par un climat méditerranéen chaud et sec (14,1 °C de température moyenne et 686 mm de précipitations) et par des pratiques de gestion du rang basées sur le désherbage chimique et les inter-rangs travaillés.

Les parcelles de l'ensemble du réseau se répartissent selon deux gradients de pratique de gestion. Un premier gradient, nommé « *gradient de perturbation physique du sol* » sépare

les parcelles dont le rang est désherbé chimiquement (absence de perturbation physique du sol) des parcelles dont les inter-rangs et les rangs sont travaillés (présence de perturbation physique du sol). Le deuxième gradient, nommé « *gradient de couverture du sol et de compétition* » discrimine les parcelles enherbées et tondues (couverture du sol et compétition élevée) des parcelles désherbées chimiquement et travaillées (faible couverture du sol et faible compétition).



**Figure 2 :** Les pourcentages de compétitivité, de tolérance aux stress et aux perturbations des communautés d'adventices des 3 régions viticoles étudiées (CA, Champagne ; LR, Languedoc-Roussillon ; RH, Vallée du Rhône). Des lettres différentes caractérisent les différences de moyennes significatives entre région (test de Wilcoxon, p-value < 0.05).

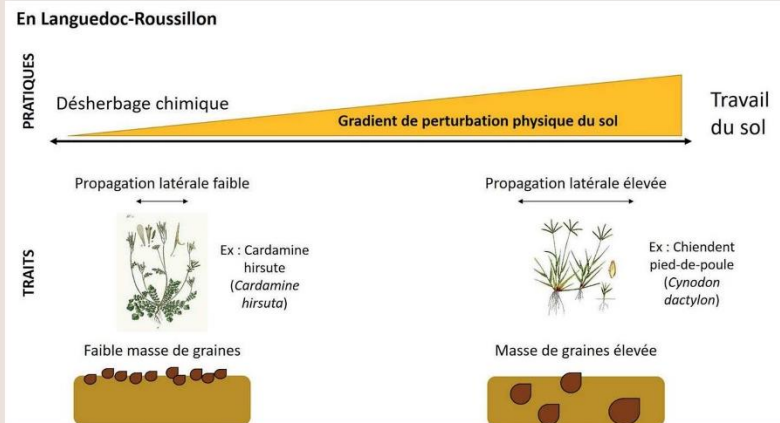
Dans les parcelles avec présence de perturbation physique du sol (travaillées), les adventices se caractérisent par des masses de graines élevées ainsi qu'une capacité de propagation latérale élevée (**Figure 3**). Les espèces à capacité de propagation latérale élevée sont les espèces à rhizomes ou à stolons (par exemple, le Chiendent pied-de-poule). Or, ces espèces sont adaptées au fractionnement par les outils de travail du sol car elles sont capables de se multiplier végétativement. Elles sont donc favorisées par le travail du sol par rapport aux espèces à faible propagation latérale qui ne se multiplient pas végétativement (par exemple, la Cardamine hirsute). De plus, les plus faibles masses des graines dans les parcelles désherbées par rapport aux parcelles travaillées peuvent s'expliquer par des positions différentes des graines dans le sol (**Figure 3**).

En effet, dans une parcelle travaillée, les graines sont enfouies dans le sol tandis qu'elles restent à la surface du sol sur une parcelle désherbées chimiquement. Or, plusieurs études ont

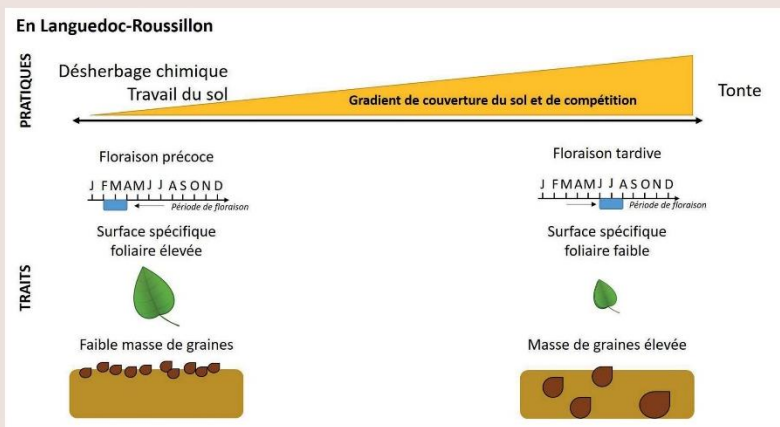
montré que les grosses graines ont une meilleure chance de germer lorsqu'elles sont dans le sol que les petites graines. De plus, la masse de graine est négativement corrélée avec le nombre de graines produites. Ainsi, dans les parcelles désherbées chimiquement, les graines produites sont plus petites mais plus nombreuses. Cette production abondante de graines permet de compenser la mortalité élevée induite par le désherbage chimique. Par ailleurs, les graines localisées en surface ont plus de chance d'être prédatées et de se dessécher. Ainsi, dans les parcelles désherbées chimiquement, produire de nombreuses petites graines permettrait de maximiser les chances que certaines puissent germer malgré les contraintes liées aux désherbages et à leur positionnement exposé.

Dans les parcelles avec une couverture de sol élevée et une compétition potentiellement plus élevée (parcelles tondues) du second gradient de pratiques, les adventices se caractérisent par une floraison tardive, une surface spécifique foliaire faible et une masse de graine élevée (**Figure 4**). Au contraire,

les parcelles à faible couverture du sol et faible compétitivité (parcelles travaillées et désherbées) sont composées d'adventices à floraison précoce, à surface foliaire élevée et à faible masse de graines. Ces caractéristiques peuvent être associées à des stratégies de tolérance face aux perturbations du milieu. En effet, dans un milieu « *incertain* » dû aux fortes perturbations comme les parcelles désherbées et travaillées, les adventices peuvent privilégier des stratégies d'acquisition de ressources (surface spécifique foliaire élevée soit la maximisation de la photosynthèse par masse de matière sèche investie), plutôt que des stratégies de conservation de ressource (surface spécifique foliaire faible). De plus, la faible masse de graines, associée à une production élevée de graines, maximise la chance que certaines puissent survivre aux perturbations que génèrent les travaux du sol et les passages de désherbants. Enfin, la floraison précoce de ces communautés peut être interprétée comme une stratégie d'évitement des perturbations : la floraison puis la production de graines ont lieu avant les passages de désherbage mécanique ou chimique.



**Figure 3 :** La réponse des traits des communautés d'adventices au gradient de perturbation physique du sol lié aux pratiques dans le Languedoc-Roussillon.



**Figure 4 :** La réponse des traits des communautés d'adventice au gradient de couverture du sol et de compétition potentielle lié aux pratiques en Languedoc-Roussillon.



## Conclusion

Les adventices s'adaptent aux pratiques de destruction (mécaniques et chimiques) et de régulation (tontes) via leurs valeurs de traits foliaires. Selon notre étude, en Languedoc, la tonte semble favoriser des espèces de type prairial, adaptées à la compétition tandis que les espèces présentes dans les parcelles travaillées et désherbées chimiquement sont des adventices couramment présentes en parcelles viticoles depuis plusieurs décennies (herbicides) ou siècles (travail du sol) aux pratiques de gestion des sols. En Champagne et dans la Vallée du Rhône, les adventices n'avaient pas les mêmes

stratégies d'adaptation aux différentes pratiques qu'en Languedoc-Roussillon, démontrant une interaction entre l'effet du pédoclimat et des pratiques. Par exemple, en Champagne et en Vallée du Rhône, les espèces présentes dans les zones tondues n'avaient pas de valeurs de traits significativement différentes que les espèces dans les zones désherbées et travaillées. Dans le Bordelais, une étude en cours de publication sur la réponse des adventices aux pratiques de gestion démontre des résultats similaires à ceux du Languedoc. La tonte favorise également les espèces adaptées à la compétition

tandis que le travail du sol est associé aux espèces tolérantes aux perturbations. Ces valeurs de traits, en particulier celles des espèces dominantes, peuvent en retour avoir une influence sur différents processus écologiques (minéralisation des nutriments, séquestration de carbone dans le sol...). Évaluer la biodiversité fonctionnelle permettrait ainsi de quantifier la contribution des adventices à la fourniture potentielle de services écosystémiques (nutrition minérale de la vigne, régulation du climat...). ■



#### POUR EN SAVOIR PLUS

L'intégralité des résultats dont cet article fait un aperçu est disponible dans l'article suivant :

**Bopp M-C, Kazakou E, Metay A, Fried G. 2022.** *Relative importance of region, seasonality and weed management practice effects on the functional structure of weed communities in French vineyards.* *Agriculture, Ecosystems & Environment* 330 : 107892.

Les deux articles suivants ont étudié l'effet des pratiques de gestion sur les espèces adventices présentes dans les vignes du même réseau :

• **Fried G, Cordeau S, Jullien J, et al. 2019.** *Flore adventice dans trois bassins viticoles.* *Phytoma. La défense des végétaux* : 34-40.

• **Fried G, Cordeau S, Metay A, Kazakou E. 2019.** *Relative importance of environmental factors and farming practices in shaping weed communities structure and composition in French vineyards.* *Agriculture, Ecosystems & Environment* 275 : 1-13.

• **Fried G, Blanchet C, Cazenave L, Bopp M-C, Kazakou E, Metay A, Christen M, Alard D and Cordeau S.** *Consistent response of weeds according to Grime's CSR strategies along disturbance and resource gradients in Bordeaux vineyards.* *Weed Research* 62:347-359.

Enfin, ce dernier article présente le cadre conceptuel sur lequel se base le cadre d'analyse de cet article :

• **Kazakou E, Fried G, Richarte J, Gimenez O, Violle C, Metay A. 2016.** *A plant trait-based response-and-effect framework to assess vineyard inter-row soil management.* *Botany Letters* 163 : 373-388.

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# **Exemple d'une fiche synthétisant les résultats restitués aux viticultrices et viticulteurs du réseau de parcelles viticoles du Montpelliérais**

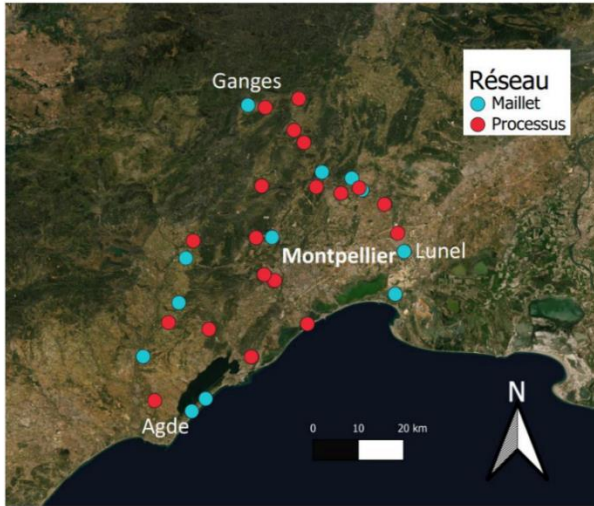
Les fiches ont été réalisées par Amélie Poulain, en stage de deuxième année d'ingénieure agronome et envoyées après la campagne de terrain de mars 2021.



# Composition floristique, caractéristiques et activités microbiennes du sol

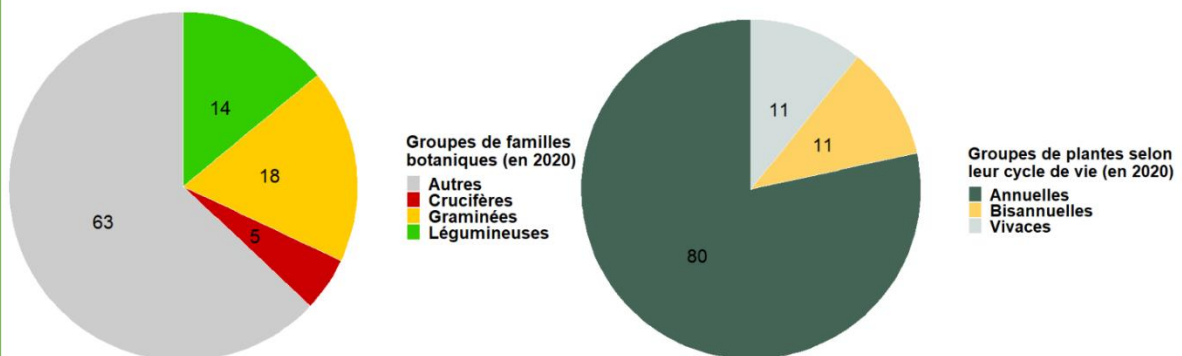
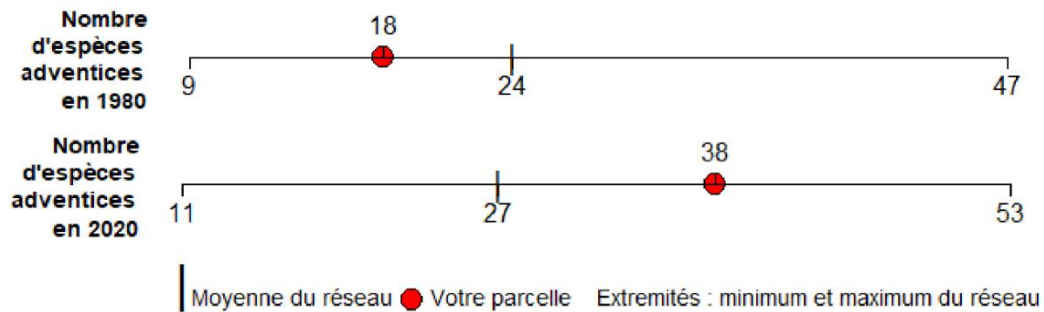
## Bilan des résultats sur votre parcelle au printemps 2020

Dans le cadre du projet SAVING\*, le but de notre travail est i) d'évaluer les changements de flore au cours du temps (depuis 1980) et ii) d'analyser comment la composition des communautés d'adventices répond aux différentes pratiques de gestion du sol. Votre parcelle fait partie d'un réseau de 40 parcelles viticoles situé dans le Montpellierais (cf. la carte du réseau ci-dessous), représentant différents modes de gestion des adventices (travail du sol, traitements chimiques ou enherbement). Voici les résultats sur votre parcelle par rapport aux autres parcelles du réseau Processus, en mars 2020. Les espèces principales sont aussi comparées à celles observées sur votre parcelle il y a 40 ans.



Ci-dessus, la localisation de nos mesures sur votre parcelle (Référence cadastrale : BY-8)

### Composition floristique de votre parcelle



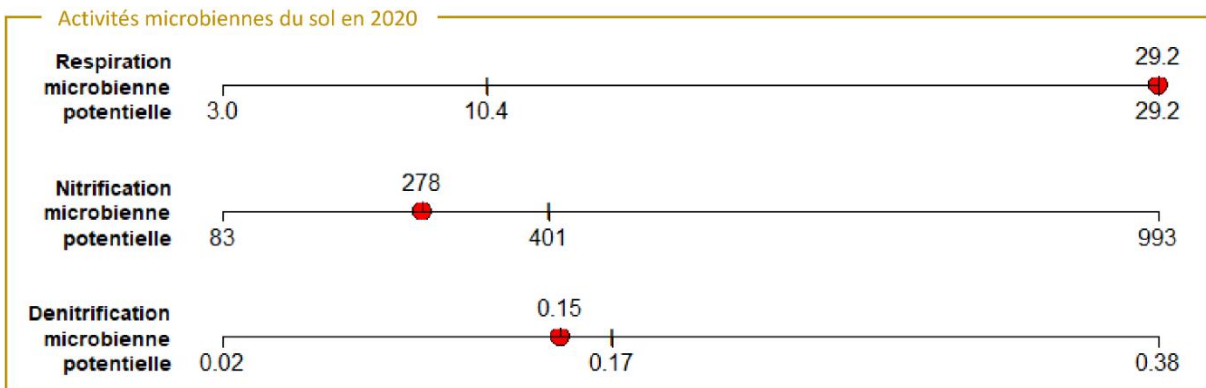
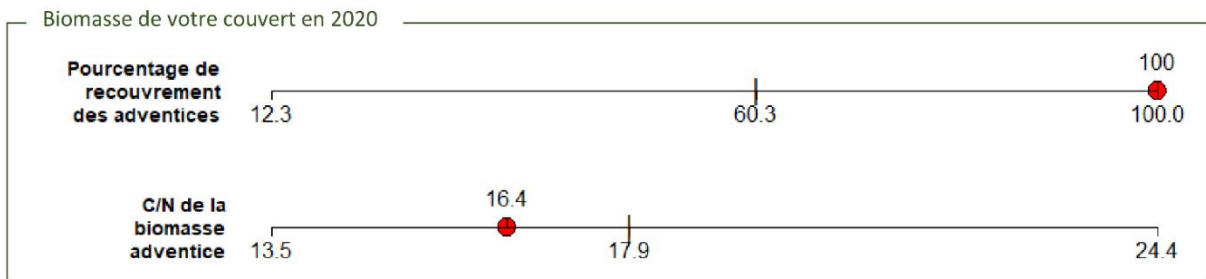




Photographie de l'espèce principale de votre parcelle en 2020 : le Brome de Madrid  
(Source : Internet)



Photographies des espèces principales de votre parcelle en 1980 : le Liseron des champs et la Crépe de Nîmes  
(Source : Internet)



## Méthodes expérimentales et interprétation

### Mesures de la biodiversité floristique :

Ces mesures ont été réalisées en mars, en juin et en octobre 2020.

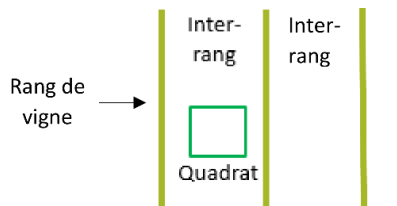
La liste des espèces présentes sous le rang et sur l'inter-rang a été établie de deux manières. La méthode de Barralis consiste à marcher sur une superficie de 400 m<sup>2</sup>

(~4 inter-rangs sur une longueur de 40 m). Cette technique permet d'avoir une vue d'ensemble de la biodiversité de la parcelle. La deuxième méthode consiste à observer des quadrats de 60x60 cm<sup>2</sup> : elle est plus précise car elle permet d'observer chaque plante et plantule.

### Mesures sur la biomasse du couvert :

- **Taux de recouvrement**

Les taux de recouvrement des inter-rangs sont estimés en positionnant un quadrat de 60x60 cm<sup>2</sup> dans quatre inter-rangs, à 10 pas du bord de la parcelle.



*Schéma de la mesure du taux de recouvrement*

- **Ratio Carbone/Azote**

Ce ratio a été mesuré à la PACE (Plateforme d'Analyses Chimiques en Ecologie) du CNRS. Si le C/N de la biomasse végétale est inférieur à 15, la vitesse de décomposition de la matière organique est élevée et de l'azote minéral est restitué au sol : le stock disponible pour la vigne augmente. Si le C/N est supérieur à 20, on observe un phénomène de « faim d'azote » : la minéralisation est lente et le stock d'azote du sol est consommé par les microorganismes, ce qui diminue la ressource azotée pour les vignes. Entre 15 et 20, le stock d'azote est stable et la matière organique peut être décomposée par les microorganismes du sol.

### Mesures des processus biochimiques du sol :

Les mesures décrites ci-dessous ont été réalisées en mars 2020, sur des échantillons de sol prélevés au milieu des quadrats de mesure de taux de recouvrement. Nous avons réalisé ces prélèvements à l'aide d'une tarière manuelle, à une profondeur de 10 cm. Les mesures de l'activité microbienne potentielle ont été réalisées en conditions contrôlées à la PACE du CNRS à Montpellier.

- **Mesure de l'activité respiratoire potentielle**

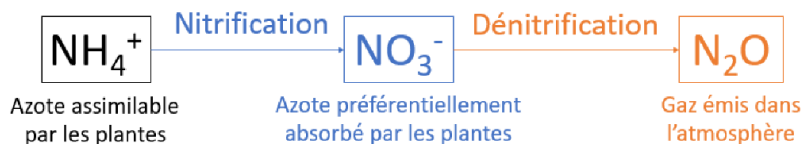
Le résultat du laboratoire donne l'activité respiratoire potentielle en microgrammes de carbone par grammes de sol sec par heure. C'est un indicateur indirect de la santé des sols et de la fourniture potentielle de nutriments. Plus la valeur est élevée, plus les bactéries, champignons et animaux du sol sont actifs.

- **Mesure de l'activité nitrifiante potentielle**

La mesure donne la nitrification potentielle en grammes d'azote par grammes de sol sec par heure. La nitrification correspond à la formation de nitrate (NO<sub>3</sub><sup>-</sup>) par la flore bactérienne du sol donc plus la valeur est élevée, plus l'ammonium (NH<sub>4</sub><sup>+</sup>) est transformé en nitrate.

- **Mesure de l'activité dénitrifiante potentielle**

Le résultat du laboratoire donne l'activité dénitrifiante potentielle des bactéries du sol, en grammes d'azote par grammes de sol sec par heure. Plus la valeur est élevée, plus l'émission de N<sub>2</sub>O (gaz à effet de serre) est importante et plus le stock d'azote du sol assimilable par les vignes diminue.



*Schéma simplifié de cycle de l'azote*



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\*Projet SAVING (Dynamique Spatio-temporelle des communautés d'espèces Adventices en réponse aux pratiques de gestion des sols dans les VlgNobles et conséquences pour la vigne : transition vers une gestion zéro Glyphosate), co-financé par la région Occitanie et l'Agence Française pour la Biodiversité, pour 3 ans à compter de septembre 2019.

## Analyses du sol de votre parcelle

Un échantillon de votre sol a été prélevé en mars 2020, puis analysé dans un laboratoire indépendant.

La case « Votre Référence » correspond à la référence de votre parcelle dans notre étude (visible sur l'image aérienne en première page du rapport). Ce numéro de référence peut être suivi d'un 1 puis d'un 2 si deux inter-rangs ont été échantillonnés : vous avez alors 4 pages de résultats d'analyses de sol (2 pages par échantillon).

Dans le cas où la référence de votre parcelle est suivie d'une lettre :

- un « E » (ou « Sc ») signifie que l'inter-rang où le sol a été prélevé était enherbé
- un « T » signifie que l'inter-rang où le sol a été prélevé était travaillé
- un « C » signifie que l'inter-rang où le sol a été prélevé était traité chimiquement

Rapport N° : 1001672

## RAPPORT D'ESSAIS

Demande N° : R-LAS-2020-09-00055

\* : Analyse réalisée sous accréditation

N° Echantillon	Votre Référence		Date Réception	Type	Sous-Type	
S-LAS-2020-01974	290		22/09/2020			
Groupe d'analyses : LAS-SOL-0102 Broyage échantillon (diamètre < 250µm)						
Méthode : NF ISO 11464						
	Réalisation	Paramètre	Unité	PA	PS	PB
*	06/10/2020	Réalisé	-	Oui		
Groupe d'analyses : LAS-SOL-0302 Granulométrie 5 fractions sans décarbonatation - g/kg						
Méthode : NF X 31-107						
	Réalisation	Paramètre	Unité	PA	PS	PB
*	30/10/2020	Argiles (0 à 0,002 mm)	g/kg	297		
*	30/10/2020	Limons fins (0,002 à 0,02 mm)	g/kg	145		
*	30/10/2020	Limons grossiers (0,02 à 0,05 mm)	g/kg	117		
*	30/10/2020	Sables fins (0,05 à 0,2 mm)	g/kg	163		
*	30/10/2020	Sables grossiers (0,2 à 2,0 mm)	g/kg	278		
Groupe d'analyses : LAS-SOL-0405 Calcaire (CaCO3) total, Carbone (C) organique, Azote (N) total - g/kg						
Méthode : NF ISO 10693, NF ISO 10694 OU NF ISO 14235, NF ISO 13878						
	Réalisation	Paramètre	Unité	PA	PS	PB
*	13/11/2020	Calcaire (CaCO3) total	g/kg	<1		
*	13/11/2020	Carbone (C) total	g/kg	19.4		
*	13/11/2020	Carbone organique total (COT)	g/kg	19.4		
*	13/11/2020	Azote (N) total	g/kg	1.71		
*	13/11/2020	C/N	g/kg	11.4		
*	13/11/2020	Matière organique	g/kg	33.6		
Groupe d'analyses : LAS-SOL-0501 pH eau						
Méthode : NF ISO 10390						
	Réalisation	Paramètre	Unité	PA	PS	PB
*	29/10/2020	pH	-	6.80		
Groupe d'analyses : LAS-SOL-0709 Extraction au chlorure de cobalthexammine						
Méthode : NF ISO 23470						
	Réalisation	Paramètre	Unité	PA	PS	PB
*	09/10/2020	Réalisé	-	Oui		
Groupe d'analyses : LAS-SOL-0710 Capacité d'échange cationique cobalthexammine (spectrocolorimétrie) - cmol+/kg						
Méthode : NF ISO 23470						
	Réalisation	Paramètre	Unité	PA	PS	PB

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## RAPPORT D'ESSAIS

Demande N° : R-LAS-2020-09-00055

\* : Analyse réalisée sous accréditation

N° Echantillon	Votre Référence		Date Réception	Type	Sous-Type	
S-LAS-2020-01974	290		22/09/2020			
Groupe d'analyses : LAS-SOL-0710 Capacité d'échange cationique cobaltihexammine (spectrocolorimétrie) - cmol+/kg						
Méthode : NF ISO 23470						
	Réalisation	Paramètre	Unité	PA	PS	PB
*	27/10/2020	CEC Effective	cmol+/kg	15.3		
Groupe d'analyses : LAS-SOL-1401 Extraction 1/10 au KCl 0.5 mol/l						
Méthode : Méthode interne						
	Réalisation	Paramètre	Unité	PA	PS	PB
	12/01/2021	Réalisé	-	oui		
Groupe d'analyses : LAS-SOL-1406 Azote minéral (N de NO3 et N de NH4) sur extrait 1/10 au KCl 0.5 mol/l - mg/kg						
Méthode : Méthode interne						
	Réalisation	Paramètre	Unité	PA	PS	PB
	24/11/2020	Azote ammoniacal (N de NH4+)	mg/kg	6.00		
	24/11/2020	Azote nitrique (N de NO3-)	mg/kg	68.2		