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Taïna Lemoine

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Taïna Lemoine. De l'ancêtre sauvage aux variétés modernes du blé dur : stratégies écologiques et réponse à la compétition. Sciences et techniques de l'agriculture. Université de Montpellier, 2023. Français. NNT : 2023UMONG110 . tel-04722482

HAL Id: tel-04722482

<https://theses.hal.science/tel-04722482v1>

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THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En Ecologie fonctionnelle et Sciences Agronomiques
École doctorale GAIA

Portée par
Centre d'Ecologie fonctionnelle et Evolutive

De l'ancêtre sauvage aux variétés modernes du blé dur :
stratégies écologiques et réponse à la compétition

Présentée par Taïna Lemoine
Le 6 décembre 2023

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UNIVERSITÉ
DE MONTPELLIER

Remerciements

Même après avoir écrit une thèse, cette partie reste la plus dure à écrire ; il m'a fallu être malade dans un train entre Lausanne et Montpellier pour enfin m'y mettre. Une partie dure à écrire car c'est le seul moment dans notre manuscrit où l'on se met à parler de sentiments humains et parler de toute cette tambouille humaine nécessite les bons mots.

Je suis la dernière thésarde de la journée du master BEE 2016-2018. Je me dois donc de commencer par remercier la ville de Montpellier. C'est dans cette ville pendant mes études que j'ai rencontrée des gens absolument formidables. C'est un long chemin qui s'achève en finalisant cette thèse et c'est avec beaucoup d'émotions que j'emporte dans ma valise les doux souvenirs de ces sept dernières années à Montpellier.

Je remercie Léo-Paul Dagallier, Maurine Hammel, Nathan Mazet, « binôme », Salmounette, mes colocos, amis pour la vie. Merci de m'avoir épaulé dans les moments difficiles de ma thèse et de ma vie en général. Merci d'être là, merci pour vos messages à la fin de ma thèse, merci pour les milliers de moments que l'on a pu vivre ensemble et qui ont participé à mon épanouissement et à mon équilibre ces dernières années. Merci pour tout cet amour.

Merci à Aurélien Chou, Aurore Chou, Alice Chou, on s'est rencontré aux différents ronds-points de ma vie, en master de biostatistiques, en stage au Cameroun ou encore à Avignon. Merci Aurélien pour ces fous rires à 8h de matin en cours de « recueil de données planifiées » où notre journée venait à peine de démarrer et on ne comprenait déjà rien ^^'. Merci pour ta gentillesse et ton écoute, j'ai tellement appris avec toi, j'ai même appris à jouer au « Qui est-ce ? » version Drag Queen. Aurore, MERCI, pour ton soutien, pour les magnifiques dessins de blé, pour tes messages doux et gentils au quotidien, et pour ces soirées folles au Cameroun en passant de la turista, aux attaques de moustiques ou encore au mille et une couleur des pagnes Africain s'agitant sur les sons rythmés du Cameroun. Merci de m'avoir porté sur la fin de l'article sur le safou sans toi je n'y serais jamais arrivée ! Alice, mon chou, on s'est rencontré à Avignon, nous partagions le même matelas gonflable de peur de se retrouver avaler dans le vieux lit moisi du propriétaire. Merci d'avoir maintenu notre lien et merci de partager mes fous rires et mes vacances chaque année.

Je souhaiterais profondément remercier Amira Azizan qui m'a maintenu en vie sur les dernières semaines de ma thèse à coup de « tu vas y arriver », de câlins et dont le sourire chaque matin au bureau m'a donné plein de courage et de force. Je souhaiterais remercier de tout mon cœur Louise Authier, mon acolyte de toujours. Nous avons fait le même master, puis je t'ai fait ton café à Tela Botanica pendant 8 mois, puis on a trouvé une thèse au CEFÉ toutes les deux, et nous voilà en train de terminer cette thèse la même semaine, le monde est bien fait.

Merci également à Thithi, Mike, Anaïs, Ana, Débo, Tomtom, Antoine pour tous les beaux moments passés ensemble et les futurs moments génialissimes qui arrivent.

Merci à mes supers copines de la danse et à ma super prof et amie Teani, sans vous mon quotidien n'aurait pas été le même. Merci de m'avoir soutenu, reboosté et de m'avoir fait danser tout au long de ma thèse <3. Merci d'ailleurs aux premiers êtres humains qui se sont mis à danser car ce sport est un réel exutoire.

Je souhaiterais remercier Stéphanie Carrière, Stan Chabert, Léo Mouillart-Lample avec qui j'ai travaillé et qui m'ont encadré durant mes stages de master. Merci mille fois car vous m'avez donné le goût de la recherche et surtout le goût du terrain dans des conditions atroces (surtout de température, avec des moutmouts), merci !!!!!!!!

Merci à mes stagiaires Elodie, Léo, Mathis et Éric. On oublie souvent que derrière les résultats des papiers et il y a de multiples petites mains. Des petites mains indispensables au fonctionnement des thèses et de la recherche en général. Merci à vous quatre d'avoir travaillé dans des conditions parfois très difficiles (n'est-ce pas Eric :P), d'avoir accepté mes erreurs, d'avoir été patient et à l'écoute. Sans vous je n'aurais pas fait cette thèse ! Merci également aux membres du TE du CEFÉ, Thierry, Pauline, Fabien, Pierrick et David avec qui l'impossible devient possible. Merci mille fois de m'avoir prêté main forte pour l'installation des différentes expériences de ma thèse. Merci à Aline Rocher qui m'a fait découvrir les joies de cultiver du blé et surtout du blé sauvage, un grand merci pour tes bons conseils et ton aide pendant le rush des récoltes. Merci pour ton efficacité redoutable et ton soutien émotionnel.

Merci à Carine Alcon qui m'a initié à l'anatomie racinaire, avec le superbe vibratome dont j'ai oublié le nom, oui car nous avons baptisé cette vieille mémère avant son départ à la retraite. Merci pour ta patience, pour tes conseils, tu as été comme une mentore pour moi.

Merci à l'équipe ECOPAR. Cette équipe est un peu comme une grande famille, tout le monde est soudé et à l'écoute. C'est une équipe pleine de vie à la fois scientifique avec les SEKOS, les multiples discussions mais aussi ludique avec les repas de Noël, les repas à la cantine, les pots de retraite, les chasses aux œufs, les journées du département. Merci aux personnes de cette équipe d'avoir égayé ces trois ans, d'avoir partagé mes états d'âme, d'avoir été gentil et à l'écoute. L'environnement de travail est central pour réussir sa thèse, merci pour tout l'équipe !! Merci à mes co-bureaux Lucie et Félix pour ces matins pittoresques, ces fracassages de petons dans les chaises égarées du bureau et nos collaborations dans le travail. Enfin, que serait un doctorant sans d'autres doctorants ? Un petit tas de gelé sans vie. Merci à Marie-Chou, Stéfania, Aurélien et Léo mes fidèles compères. Merci pour ces discussions sur nos manips qui ne marchent pas ou nos résultats qui ne veulent rien dire, merci pour nos discussions sur le bien-être, merci d'avoir été à l'écoute et de m'avoir remotivé quand ça n'allait pas. Merci pour les soirées robes, les balades sur le TE, les bières au drapeau rouge, et j'en passe. MERCI !!

Je souhaiterais grandement remercier les membres de mon comité de thèse Vincent Allard, Michel-Pierre Faucon, Marie-Laure Navas et Alexia Stokes avec qui les discussions ont été riches et très stimulantes pour ma thèse. Le premier comité de thèse m'avait énormément stressé, ne vous connaissant pas, mais j'ai vite compris dès les premières minutes d'échanges que l'atmosphère serait bienveillante et vos conseils très utiles. Merci !

Je souhaiterais remercier chaleureusement les membres de mon jury, Anne Laperche, Joëlle Fustec, Maud Tenaillon, Olivier Duchene et Philippe Hinsinger d'avoir accepté de lire et d'évaluer mon travail de thèse.

Le moment est venu de remercier les personnes sans qui cette thèse n'aurait jamais eu lieu. Je remercie de tout mon cœur mes trois directeurs de thèse Cyrille, Hélène et Florian. Cyrille cette aventure a commencé grâce à toi et à un peu Aurélien quand même. Un concours de circonstance, et me voilà embarqué dans cette aventure avec vous. Merci d'avoir cru en moi, alors que je ne parlais avec aucune base en écologie fonctionnelle. Merci de m'avoir soutenu dans les moments difficiles en me grondant à moitié quand je ne me faisais pas assez confiance. Merci de m'avoir encouragé dans l'écriture scientifique, dans la pratique de l'anglais à l'oral et de m'avoir poussé dans plein de projets différents.

Tu es un peu l'homme avec une idée à la seconde mais tu es aussi extrêmement attentif au bien-être dans l'équipe et des gens en général, merci pour ça. Hélène, merci pour ta douceur, ta bonne humeur et ta rigueur. Merci de m'avoir apporté pleins de nouvelles idées et d'avoir amené un autre regard sur mon travail celui de la biologie évolutive et de la génétique. Je ne peux pas ne pas écrire cette dernière aventure que nous avons eu, « l'aventure du scan-chevelu », lorsqu'un de tes cheveux s'est immiscé dans le scan des signatures pour la demande de soutenance de thèse à Gaia hihhi. Florian, toujours là, toujours à l'écoute, toujours disponible, merci de m'avoir écouté déblatérer des bêtises, d'avoir rigolé avec moi, de m'avoir remotivé dans les moments où ce n'était pas trop la joie. Tu es un super encadrant ! Merci d'avoir mis la main à la pâte dans les manips et d'avoir encore déterré et lavé à grande eau des racines, à croire que tu adores les racines :P. Merci à vous trois, vous formez une super équipe, très complémentaire et les futurs doctorants auront de la chance de vous avoir.

Je souhaiterais maintenant remercier ma famille. C'est une famille plutôt atypique, un peu vagabonde, qui a un amour absolument effroyable du soleil et des îles. Merci Maman, Papa, de m'avoir donné tout votre amour, de m'avoir donné toutes les bonnes choses pour faire de moi un être fonctionnel (héhéhé). Merci à ma petite sœur, mon âme-sœur, tu es la personne que j'aime le plus au monde. Merci d'être mon acolyte depuis le début de notre vie et merci d'être là à chaque moment de ma vie. Merci à ma mamie, de m'avoir soutenu émotionnellement et financièrement pendant mes années à la fac. Si tous les étudiants avaient une mamie comme toi, aucun n'aurait à travailler à Carrefour City pour payer ces études et on partirait tous avec les mêmes chances pour réussir à la fac.

Ça fera le 72eme merci de ces remerciements mais s'en est un très important... Arthur, je n'ai pas de mots pour te dire à quel point tu es important dans ma vie et à quel point tu as été central dans ma thèse. Tu m'as entendu me plaindre peut-être 1000000000 fois et pourtant tu as toujours trouvé les mots, tu m'as toujours réconforté, remotivé...Merci d'être là, merci pour ces discussions de biologie endiablées, merci pour tout ce que tu fais pour moi.

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Avant-propos

Les plantes domestiquées sont devenues pour une minorité d'entre elles le socle de l'alimentation mondiale. En effet, seulement une quinzaine d'espèces de plantes représente plus de 90 % des besoins énergétiques pour une majorité d'humains (Gepts, 2006). L'agriculture moderne a profondément changé les systèmes de production alimentaire et a joué un rôle central pour la sécurité alimentaire au cours du dernier siècle (Evenson & Gollin, 2003). Pour autant, les sociétés humaines doivent actuellement relever un certain nombre de défis concernant la productivité, la stabilité et la résilience des systèmes cultivés (Tilman, 1999). En effet, produire plus pour une population mondiale croissante, tout en diminuant les impacts de l'agriculture sur l'environnement, dans un contexte de changement climatique constitue un réel défi. Par ailleurs, durant le XX^e siècle, l'érosion génétique des ressources génétiques des cultures est devenue un sujet de préoccupation pour les sélectionneurs (Gepts, 2006). La domestication et l'amélioration variétale ont conduit à une forte réduction des niveaux de diversité génétique et phénotypique au sein des variétés modernes par rapport à leurs parents sauvages (Day, 1973; Gepts, 2004; Reif *et al.*, 2005; Glémin & Bataillon, 2009). Une part importante de la production alimentaire mondiale repose donc sur l'utilisation de variétés mono-génotypiques génétiquement peu diversifiées. Ces variétés peu diversifiées et adaptées à des milieux artificialisés arriveront-elles à s'adapter aux nouveaux agrosystèmes (changements de pratiques, faible niveau en ressources) et aux changements globaux (Lesk *et al.*, 2016)? Pour répondre aux défis de stabilité, de productivité et de résilience des agrosystèmes, il a été proposé d'améliorer les fonctions écosystémiques de ces systèmes (Altieri, 1989; Wezel *et al.*, 2009). Cela passe notamment par l'augmentation de la diversité dans les agrosystèmes en termes de nombre d'espèces ou de génotypes (Tilman, 2001; Barot *et al.*, 2017; Gross *et al.*, 2017). Il est également de plus en plus envisagé de diversifier le matériel végétal cultivé en utilisant la diversité génétique contenue dans les ancêtres sauvages des cultures ((Dempewolf *et al.*, 2017; Zhang *et al.*, 2017). Intégrer des approches pluridisciplinaires en écologie et en évolution semble alors primordial pour relever les défis associés aux cultures (Montazeaud, 2019). De plus, les espèces cultivées constituent un réservoir incroyable de connaissances pour l'écologie et l'évolution. Les changements phénotypiques qu'ont connus nos cultures depuis leur état sauvage jusqu'aux cultivars modernes reflètent les multiples pressions de

sélection associées à l’histoire de domestication et de sélection des cultures. Ces changements sont aussi la preuve que les espèces cultivées se sont adaptée depuis des milliers d’années aux différentes conditions abiotiques et biotiques des environnements cultivés. Analyser les changements phénotypiques qui ont opéré au cours de la domestication et de la sélection moderne peut permettre de décrire les liens entre phénotype et processus écologiques au sein des agroécosystèmes et de participer à orienter les programmes de sélection et les pratiques agricoles.



L'homme au grand nez

INTRODUCTION

I. Les traits fonctionnels pour étudier l'évolution des espèces cultivées

Les études génétiques et archéologiques ont fortement contribué à la compréhension de l'histoire évolutive des cultures et des contraintes qui les ont façonnées (Meyer & Purugganan, 2013; Larson *et al.*, 2014). Récemment, l'écologie, a fourni un cadre complémentaire et pertinent, pour appréhender les changements phénotypiques au cours de la domestication et de la sélection moderne, et comprendre leurs effets sur les processus écologiques¹ au sein des systèmes cultivés (McKey *et al.*, 2012; Milla *et al.*, 2015).

L'écologie fonctionnelle s'attache à décrire et à comprendre les patrons de diversité phénotypique à différentes échelles d'organisation et dans différents environnements (Garnier *et al.*, 2016). Cette discipline intègre une dimension comparative qui s'attache à décrire la réponse d'un grand nombre d'espèces ou de génotypes à différents environnements. L'approche comparative permet de capter un patron général, qui ne résulte pas seulement de particularités de réponse au milieu des quelques espèces étudiées (Keddy, 1992). L'écologie fonctionnelle est généralement présentée comme un prolongement de l'écophysiologie (Duarte *et al.*, 1995). La caractérisation fonctionnelle s'appuie sur la mesure à l'échelle individuelle de caractéristiques morphologiques, phénologiques, physiologiques, aussi appelé « traits » (Violle *et al.*, 2007) (Fig. 1). Les traits (ex. taille des graines, hauteur, surface foliaire) sont des marqueurs fonctionnels étroitement liés à la croissance, à la survie et à la reproduction de l'organisme. Les traits fonctionnels permettent à la fois d'expliquer la réponse des plantes aux variations environnementales (« traits de réponse ») et l'effet des plantes sur les fonctions et les services d'une communauté et d'un écosystème (« traits d'effet ») (Lavorel & Garnier, 2002). Les traits fonctionnels mesurés à l'échelle de l'organe ou de l'individu contribuent à expliquer la valeur sélective² des organismes, nommés traits de performance (par exemple chez les plantes, le nombre de graines, la biomasse végétale ; Fig. 1; Violle *et al.*, 2007).

¹ Les processus écologiques ici sont définis comme l'ensemble des processus ou des mécanismes qui évoluent et lient les organismes et leur environnement (abiotique et biotique).

²La valeur sélective ou aussi appelé « fitness » décrit la capacité des organismes — ou, plus rarement, des populations ou espèce - à survivre et à se reproduire dans l'environnement dans lequel ils se trouvent (Orr, 2009).

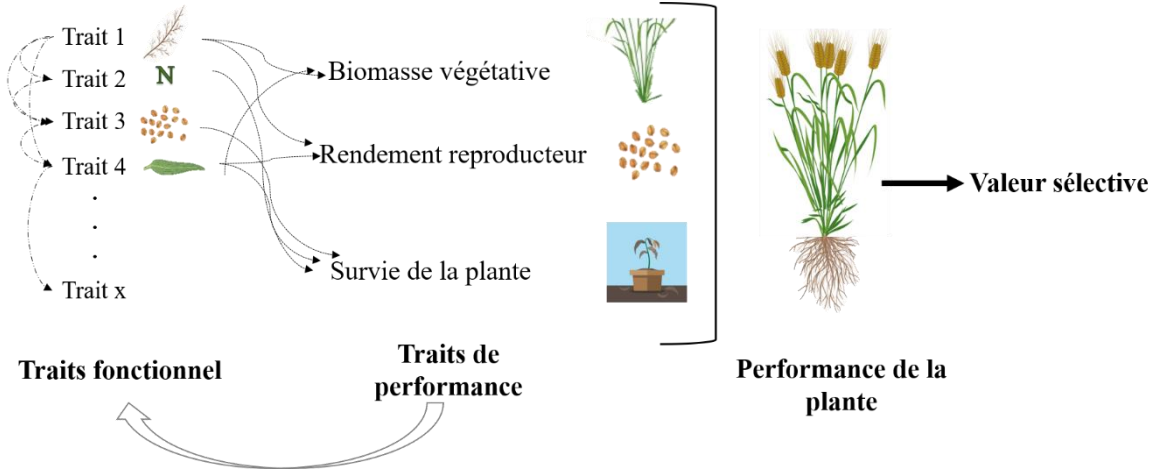


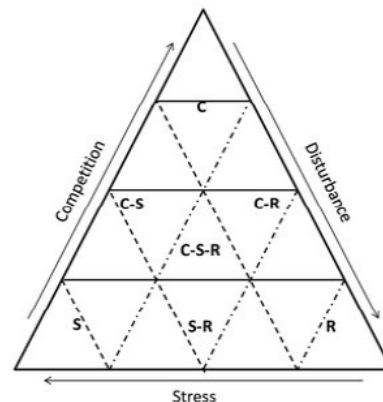
Figure 1. Les traits fonctionnels aériens ou racinaires de 1 à x (morphologique, phénologique et physiologique) interagissent et modulent les traits de performance qui sont la biomasse végétative, le rendement reproducteur et la survie de la plante. Les traits de performance déterminent la performance de la plante et indirectement la valeur sélective des individus. Les variations des traits de performance peuvent en retour moduler les traits fonctionnels. Par exemple, une diminution de la taille d'une plante peut s'expliquer par une diminution de la biomasse végétative. Les interdépendances entre les traits de performance ne sont pas montrées. Adaptée de Violle *et al.*, (2007).

Dans le cadre d'une espèce cultivée, les traits fonctionnels ont été proposés comme de potentiels prédicteurs de la performance agronomique des espèces cultivées, en particulier du rendement en grains (Martin & Isaac, 2015; Gagliardi *et al.*, 2015; Rolhauser *et al.*, 2022; MacLaren *et al.*, 2023). La performance agronomique est classiquement décrite par plusieurs traits agronomiques tels que le rendement en grains, le nombre d'épis par m², le nombre de graines par épi et le poids de mille grains (Bulman & Hunt, 1988; Kozak & Mądry, 2006). L'approche fonctionnelle va permettre de caractériser les traits fonctionnels associés à la croissance des plantes cultivées et au rendement reproducteur, deux fonctions impliquées dans la variation des traits agronomiques (Barai *et al.*, 2022). Cependant, le potentiel prédictif de la performance agronomique par les traits fonctionnels aériens et souterrains reste encore peu exploré, notamment par des approches multi-traits en conditions au champ.

Les approches comparatives qui s'appuient sur l'analyse des traits fonctionnels ont permis d'expliquer la réponse des plantes à leur milieu, et, plus généralement, de décrire des stratégies écologiques pour l'ensemble du monde végétal (Grime, 1979; Westoby, 1998). Une stratégie écologique est définie par Craine (2009) comme un ensemble d'adaptations phénotypiques résultant de l'effet de la sélection naturelle conduisant à une augmentation de la valeur sélective des espèces dans un environnement donné. Les stratégies écologiques sont déterminées par différents axes de variation phénotypique, structurés suivant des compromis³ écophysologiques. En effet, les plantes acquièrent des ressources en quantités limitées (carbone, eau, nutriments), puis les stockent ou les allouent à un organe en particulier (feuilles, racines, tiges, graines) les amenant à faire des compromis. Plusieurs compromis écophysologiques (par exemple entre croissance et survie des plantes : Bloom, Chapin, et Mooney 1985; Reich 2014) existent chez les plantes et contraignent leur diversité phénotypique (Garnier *et al.*, 2016). Le triangle de Grime (C-S-R, Grime, 1977) est un des modèles pionniers, encore influent aujourd'hui (Encadré 1).

Encadré 1 - Le triangle de Grime décrit les stratégies écologiques chez les plantes en réponse à deux facteurs environnementaux : la quantité de ressources et la perturbation

Selon Grime, les espèces sont contraintes soit de croître rapidement et d'exploiter les **ressources** disponibles, soit de croître lentement et de tolérer un niveau de stress élevé. Il discrimine les espèces « **compétitives** » (C) et « **tolérantes au stress** » (S) (classification C-S). La **rudéralité** (R), stratégie majeure des espèces annuelles, s'oppose à ces deux premières stratégies et constitue un **gradient de réponse à la perturbation** avec, d'un côté, des espèces peu tolérantes à la perturbation (vers C et S) et de l'autre des espèces qui la tolèrent (R). Des algorithmes pour quantifier ces stratégies ont été développés ces dernières années (Pierce *et al.*, 2017).



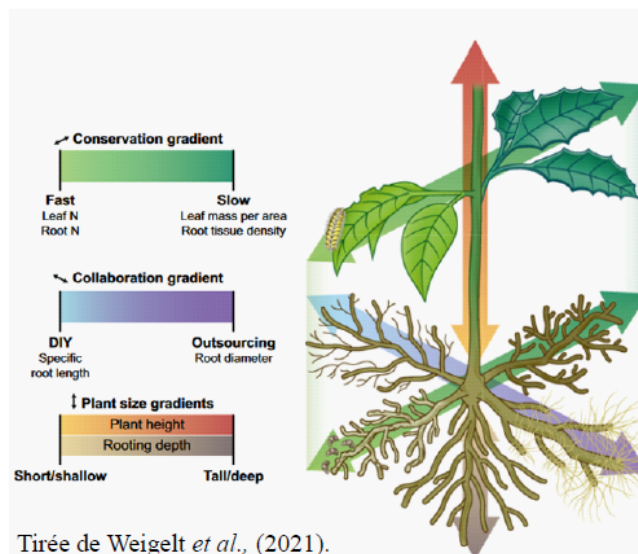
³ Un compromis implique une contrainte placée simultanément sur la relation fonctionnelle entre deux (ou plusieurs) traits (Garland *et al.*, 2022).

Des études récentes ont permis d'identifier certains des principaux axes de variation phénotypiques interspécifiques pour le compartiment aérien et souterrain (Díaz *et al.*, 2016; Bergmann & Weigelt, 2020; Weigelt *et al.*, 2021). Díaz *et al.*, (2016) ont résumé la variation phénotypique de milliers d'espèces de plantes vasculaires par un espace phénotypique à six traits. Les auteurs ont identifié deux principaux axes de variation, un premier axe de taille, qui discriminait les espèces herbacées de petites tailles à petites graines, des grands arbres à grosses graines, et un second axe caractérisant un compromis foliaire d'acquisition-conservation des ressources, mieux connu sous le nom de « Leaf Economic Spectrum » (LES) (Wright *et al.*, 2004; Reich, 2014). Ce dernier discrimine, des espèces à feuilles dites « acquisitives » (haute teneur en azote, peu épaisse) à métabolisme photosynthétique rapide, mais de courte durée de vie, des espèces à feuilles dites « conservatives » (faible teneur en azote, très épaisse) caractérisées par un métabolisme lent et une longue durée de vie. Pour le compartiment racinaire, plusieurs études ont établi des similitudes fonctionnelles entre les traits aériens et souterrains leur permettant de définir un axe de variation unique d'acquisition-conservation des ressources intégrant les feuilles, les tiges et les racines (Freschet *et al.*, 2010; Reich, 2014; Riva *et al.*, 2016). Cependant, plusieurs études ont proposé que la variation expliquée des traits racinaires observée entre les espèces ne pouvait pas être simplement expliquée par un seul axe de variation compte tenu de la complexité de l'environnement souterrain (Kramer-Walter *et al.*, 2016; Bergmann & Weigelt, 2020; Weigelt *et al.*, 2021; Carmona *et al.*, 2021). Weigelt *et al.* (2021) ont donc par la suite proposé une approche intégrative de la forme et de la fonction des plantes (Encadré 2).

Encadré 2 - Une approche intégrative de la forme et de la fonction des plantes - reliant les traits aériens et souterrains

Quatre axes de variation :

- Deux axes principaux représentant pour le premier, un **compromis foliaire et racinaire d'acquisition-conservation des ressources** et pour le second, un **axe de stratégie d'exploration du sol** ou axe de « collaboration ».
- Deux axes orthogonaux supplémentaires reliés à la **taille en hauteur** des plantes et à la **profondeur d'enracinement** on également été mis en évidence (Weigelt *et al.*, 2021).



L'axe de stratégie d'exploration du sol, oppose d'un côté des espèces, efficaces pour explorer le sol et acquérir des ressources via des racines fines et bon marché et, de l'autre, des espèces à racines épaisses qui investissent plus de carbone dans l'exploration des sols et collaborent avec des partenaires mycorhiziens (Bergmann et Weigelt, 2020).

Les plantes cultivées ont subi au cours des millénaires de profonds changements génétiques et phénotypiques qui résultent de l'action de trois pressions de sélection simultanées : la sélection intentionnelle (artificielle), la sélection non-intentionnelle (naturelle) et la sélection indirecte (Milla *et al.*, 2015) (Fig. 2). Les sociétés humaines ont donc mené des actions réfléchies et choisies, qui ont amené à la mise en place et à la gestion de différents systèmes agricoles, et à la sélection de particularités phénotypiques qui caractérisent les cultures d'aujourd'hui (Abbo *et al.*, 2014a). Les changements génétiques et phénotypiques des cultures impliquent par ailleurs des pressions de sélection non-intentionnelles. Ces dernières résultent de l'adaptation des espèces cultivées aux environnements façonnés par l'homme et aux diverses pratiques culturales liées à la préparation du sol, à la récolte et à la transformation des cultures (Zohary, 2004; Purugganan & Fuller, 2009; Fuller *et al.*, 2010). Enfin, la sélection indirecte suppose que la sélection d'un trait A peut conduire à la sélection indirecte d'un trait B en raison des corrélations entre les traits. Ces traits, étant liés ensemble, peuvent alors être sujets à des modifications de leur expression ou de leur valeur par la sélection d'un trait d'intérêt qui leur est corrélé (Gallais, 1984; Phillips & Arnold, 1989). Ceci

montre que les changements phénotypiques qui ont opéré au cours de l'histoire évolutive des cultures ont été contraints par l'existence de contraintes biophysiques, écophysiological ou génétiques (pléiotropie⁴ par exemple) entre les traits (Milla *et al.*, 2015; Garland *et al.*, 2022). L'écologie fonctionnelle peut donc permettre d'appréhender les changements de stratégies écologiques qui ont opéré au cours de la domestication et de la sélection moderne. Cette approche peut aussi permettre de comprendre comment les espèces cultivées ont répondu et se sont adaptées aux différents environnements de culture.

Approche en écologie qui s'appuie sur les traits

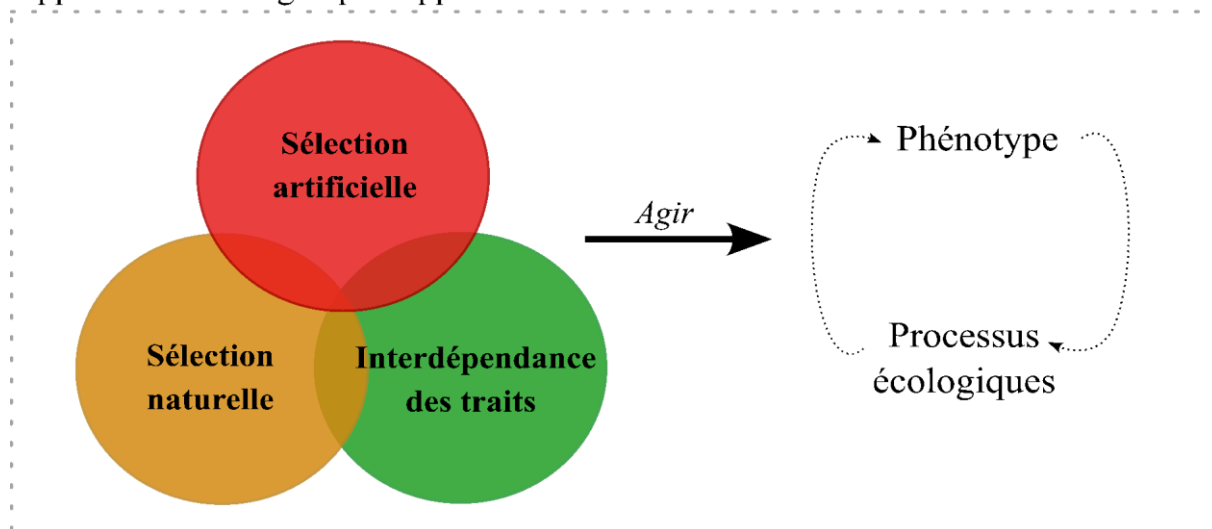


Figure 2. Schéma représentant les trois pressions de sélection simultanées, qui ont agi et agissent sur le phénotype des cultures et par rétroaction sur les processus écologiques des écosystèmes cultivés. La sélection artificielle ou intentionnelle pour des traits agronomiques d'intérêt a modulé le phénotype des espèces cultivées. La sélection naturelle ou non intentionnelle a agi sur le phénotype des espèces cultivées qui ont dû s'adapter aux environnements des cultures façonnés par l'homme. Les corrélations entre traits ou interdépendance supposent que la sélection directe d'un trait A peut engendrer la sélection indirecte d'un trait B. L'écologie fonctionnelle constitue un outil pour appréhender les conséquences de l'évolution des cultures sur le phénotype et les processus écologiques. Adaptée de Milla *et al.*, (2015).

⁴ Multiples effets phénotypiques d'un seul gène ou d'une paire de gènes.

| Les limites de connaissances

- ❖ Combien de traits et quels traits sont nécessaires pour capturer les différentes stratégies écologiques chez les plantes ?
 - ❖ Quelles sont les combinaisons de traits qui prédisent le mieux la performance d'une plante et la performance agronomique ?
 - ❖ Comment ont varié les stratégies écologiques des espèces cultivées au cours de la domestication et de la sélection moderne ?
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II. Comment ont évolué les environnements des cultures ?

Il y a environ dix à douze mille ans, dans différentes parties du monde, les sociétés de chasseurs-cueilleurs sont progressivement devenues des sociétés sédentaires agricoles, marquant le début de la domestication et de la dépendance entre êtres humains et cultures (Diamond, 2002). La domestication est définie comme un processus de coévolution découlant d'une relation de mutualisme, au sein de laquelle le « domestiquant » impose et contrôle l'environnement et donc la valeur sélective (survie, croissance, reproduction) du « domestiqué », dans le but qu'il fournisse des ressources et/ou des services (Purugganan, 2022). Les ancêtres sauvages des cultures ont été déplacés de leurs habitats d'origine, où initialement les humains pratiquaient la cueillette (Weiss *et al.*, 2006), et amenés dans de nouveaux environnements créés et gérés par ces derniers. Les conditions environnementales des systèmes cultivés, depuis le Néolithique⁵ à nos jours ont fortement varié.

En 1916, Engelbrecht s'intéresse à l'origine des espèces cultivées et propose une hypothèse, l'hypothèse « Dump Head » ou « Première décharge » (Fig. 3). Cette hypothèse suggère que les hommes ont, dans leur recherche de nourriture, ramené au camp, des graines, des fruits ou des tubercules pour les consommer, et les ont jetés à proximité des habitations et des tas d'ordures (Zeven, 1973; Hawkes, 2013). Au sein de cet environnement anthropisé, fertile et perturbé, une

⁵ Le Néolithique, succédant au Mésolithique, est une période marquée par d'importants changements techniques et sociaux-culturels avec l'adoption de l'agriculture et de l'élevage, la sédentarisation des sociétés humaines et l'apparition d'innovations techniques comme la poterie ou le tissage.

flore rudérale s'est progressivement développée. Les plantes sauvages d'intérêt alimentaire ou pour d'autres usages, du fait d'une plus forte fertilité de ces sols, ont pu produire une plus forte biomasse végétative et quantité de graines que leurs homologues dans les conditions d'origine. Une meilleure aptitude à la compétition des ancêtres des cultures du fait d'une meilleure adaptation à ces milieux a pu également leur permettre d'y être plus abondant (Cunniff *et al.*, 2014). Ces espèces, par leur abondance et leur productivité à proximité des habitations ont été ensuite adoptées comme culture (Rindos *et al.*, 1980). L'aspect « non intentionnel » de l'origine des espèces cultivées est remis en question par certaines études. Elles considèrent qu'il ne faut pas sous-estimer l'intentionnalité humaine dans la transition Néolithique (Abbo *et al.*, 2005).

A partir de l'analyse isotopique du carbone et de l'azote dans des fossiles de graines et de charbon chez des variétés de blé et d'orge anciennes et modernes, Araus *et al.* (2014) ont montré que le début de l'agriculture s'est déroulé dans des conditions environnementales très favorables, dans des milieux aux sols humides et fertiles. Ces habitats riches en nutriments ont été montrés comme majoritairement exploités par des espèces compétitives et rudérales comme les cultures herbacées (Chapin, 1980). Des preuves archéobotaniques sur les communautés d'adventices qui accompagnaient les cultures en Europe centrale au Néolithique, ont également identifié des conditions pédologiques hautement productives et perturbées (Bogaard *et al.*, 2013). Ces preuves vont dans le sens d'une mise en place progressive de pratiques de gestion comme l'apport de fumier et d'eau par les premiers agriculteurs. Des pratiques de culture mêlant des légumineuses et des céréales ont également été proposées pour expliquer le maintien d'une fertilité importante dans les systèmes cultivés permanents en Europe Centrale (Saqalli *et al.*, 2014). En revanche, il a été montré une diminution progressive des isotopes de l'azote et du carbone avec la domestication et une fluctuation des niveaux hydriques associée aux événements climatiques majeurs (Araus *et al.*, 2014). La perte progressive de fertilité des sols pourrait résulter des pratiques de l'agriculture continue (sans jachères), de l'établissement des zones agricoles sur des zones moins fertiles, ou encore de la réduction d'apport de fumier (Araus *et al.*, 2014). En Europe, l'agriculture de subsistance reposerait sur un modèle agricole de type « jardin » à petite échelle, proche des lieux de vie, impliquant une gestion intensive (jachère courte) et une main d'œuvre importante par unité de surface cultivée (Bogaard, 2005; Jones, 2005) (Fig. 3). Compte tenu de la densité de la population qui peuplait ces zones, la densité des semis était probablement faible (Saqalli *et al.*, 2014). Lee *et al.*, (2007) ont montré, en Chine, des changements dans la densité de graines entre le

début et le milieu du Néolithique, suggérant une augmentation de l'intensité de la production agricole entre ces deux périodes. Les espèces domestiquées ont progressivement été cultivées en peuplements plus denses et ont atteint des densités maximales avec l'agriculture moderne (Fischer & Edmeades, 2010).

A l'opposé de l'agriculture de subsistance, l'agriculture intensive moderne (Fig. 3) a entraîné d'importants changements dans les systèmes cultivés. Le milieu du XX^{ème} siècle est marqué par une intensification de l'agriculture pour répondre aux besoins alimentaires croissants des populations dans de nombreux pays (Khush, 2001). Le système agricole dominant, appelé diversement agriculture conventionnelle, moderne ou industrielle, a permis une augmentation considérable de la productivité et de l'efficacité agricole (Gold, 1999). L'agriculture intensive moderne a conduit à une importante conversion des écosystèmes naturels ou semi-naturels en terres cultivées (Tilman *et al.*, 2001). Elle se caractérise aussi par des apports intensifs d'engrais chimiques et de pesticides et une augmentation de la densité des semis (par exemple, entre 1930 et 2010, la densité de semis du maïs est passée de 3 plantes par m² à 8 plantes par m²; Mansfield & Mumm, 2014). L'application importante de fertilisant et la forte dégradation physique et chimique des sols (labour intensif) durant la Révolution Verte a toutefois engendré une dégradation de la fertilité des sols (Tilman, 1998; Singh, 2000). De plus, les systèmes cultivés modernes consistent majoritairement en la culture d'une seule espèce et n'inclut pas ou peu de diversité génotypique (Bourke *et al.*, 2021), contrairement aux systèmes agricoles traditionnels où des niveaux élevés de diversité à différents niveaux biologiques sont maintenus (Vargas-Ponce *et al.*, 2009). Les environnements des cultures ont fortement varié, depuis les prémices de l'agriculture, tant dans leurs conditions abiotiques (nutriments, eau) et biotiques (plante voisine et densité des semis) que dans les pratiques de gestions associées (irrigation, fertilisation, labour, rotations des cultures). On peut donc s'attendre à des changements dans les stratégies écologiques des espèces cultivées au cours de la domestication (Fig. 3).

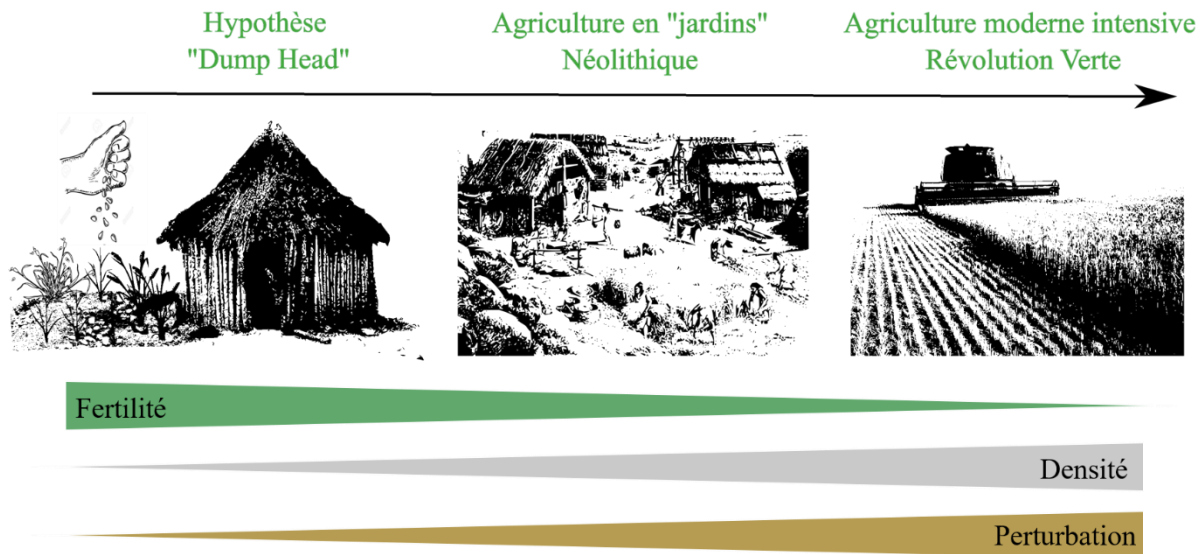


Figure 3. Représentation schématique de l'évolution des conditions environnementales des milieux cultivés. Les changements dans la fertilité, la perturbation et la densité dans les milieux cultivés au cours de l'évolution des cultures illustrés ici ont été construits à partir de ce qui a été démontré dans les différentes études (Khush, 2001; Jones, 2005; Lee *et al.*, 2007; Bogaard *et al.*, 2013; Mansfield & Mumm, 2014; Saqalli *et al.*, 2014; Araus *et al.*, 2014). Ces paramètres sont probablement dépendants de multiples facteurs (espèce cultivée, zone géographique, ...). Ces conditions n'ont donc potentiellement pas varié linéairement dans le temps et l'espace. La frise d'images a été créée en transformant des images originales provenant du journal Le Monde, Histoire et civilisations (AKG-IMAGES / CHRISTIAN JEGOU PUB) et du blog (destins-de-chasseurs-cueilleurs-les-bushmanmythe-et-histoire).

III. Des ancêtres sauvages aux premières formes domestiquées

Parmi les 369 000 espèces d'Angiospermes, un faible nombre d'espèces de plantes (environ 2500) furent domestiquées (Zeven & Wet, 1982). Parmi elles, se trouve une grande proportion d'espèces de graminées (environ 15% ; Zeven & Wet, 1982), dont le blé (*Triticum spp.*) et l'orge (*Hordeum vulgare*), premières représentantes de la domestication chez les céréales (Zohary & Hopf, 2000). De nombreuses études s'attachent encore à comprendre pourquoi et comment ces espèces en particulier sont devenues le socle de notre alimentation (Meyer *et al.*, 2012; Preece *et al.*, 2015, 2018; Gepts, 2004). Les caractéristiques partagées entre les premières espèces domestiquées comme les cycles de vie annuelles et l'autogamie suggèrent que certaines espèces pouvaient être

plus propices à être domestiquées (Gepts, 2004; Glémin & Bataillon, 2009). La quantité de grains produits en peuplement aurait également été un facteur important dans le choix des espèces cultivées (Zeven, 1973). En effet, il a récemment été montré qu'en conditions de forte compétition, l'effort reproducteur, correspondant à la part de biomasse allouée à la reproduction, était plus important chez les ancêtres des cultures que chez les autres espèces sauvages (Preece *et al.*, 2018). Récemment, il a été montré que les ancêtres sauvages des cultures avaient une plus grande stature (Cunniff *et al.*, 2014) et des activités métaboliques et photosynthétiques foliaires plus élevées que les autres espèces herbacées annuelles (Gómez-Fernández, 2023). Par ailleurs, Martín-Robles *et al.*, (2019) ont montré que les ancêtres sauvages des cultures présentaient des racines plus épaisses et peu denses, caractéristiques d'un faible investissement structurel dans les racines, par rapport à d'autres espèces sauvages. Ces traits racinaires ont été discutés par les auteurs comme typiques des plantes se développant dans des milieux fertiles (voir Poorter & Ryser, 2015). L'ensemble de ces résultats suggèrent que le « choix » des espèces domestiquées reposerait au moins en partie sur leur capacité à s'adapter à un milieu compétitif et perturbé (Mercuri *et al.*, 2018; Jones *et al.*, 2021) et donc probablement sur d'autres traits comme la taille et le port de la plante, la taille des grains ou encore l'architecture racinaire (Cunniff *et al.*, 2014; Preece *et al.*, 2018; Martín-Robles *et al.*, 2019).

La domestication des espèces sauvages a façonné la diversité génétique et phénotypique des espèces domestiquées (Harlan *et al.*, 2012). La coévolution entre l'espèce humaine et les espèces domestiquées a donné lieu à un ensemble de traits héréditaires, partagés entre les différentes espèces domestiquées, définies sous le terme de « syndrome de domestication » (Darwin, 1868; Harlan *et al.*, 1973). En effet, les pressions de sélection, liés aux environnements de cultures et aux pratiques agricoles, ont conduit à des adaptations similaires chez une large gamme d'espèces (Fuller, 2007; Meyer *et al.*, 2012). Une étude récente a d'ailleurs montré que les mammifères et les plantes domestiquées occupaient une partie spécifique et réduite de l'espace phénotypique occupés par leurs homologues sauvages, et partageaient des traits en communs (Milla *et al.*, 2018). Un ensemble de traits liés à la récolte, à la productivité et à la compétitivité des plantes notamment au stade semis s'est donc progressivement fixé au cours de la domestication respective d'un grand nombre d'espèces (Harlan *et al.*, 1973; Glémin & Bataillon, 2009)(Fig. 4). La sélection de ces traits s'explique par des changements de pratique, et en particulier par le fait que les humains se sont mis

à semer une part des graines qu'ils récoltaient. Le début de la mise en place de système de production alimentaire par le travail du sol et par le choix des semences a aussi imposé d'importantes pressions de sélection sur les espèces cultivées les rendant plus productives (Fuller, 2007).

Le syndrome de domestication chez les plantes se caractérise par une disparition de la capacité à disperser, une augmentation de la taille des organes récoltés (graine, fruit, racine), une levée de la dormance des graines, une stature moins ramifiée, et une diminution des défenses physiques et chimiques (Meyer *et al.*, 2012; Meyer & Purugganan, 2013) (Fig. 4). Un des changements phénotypiques emblématiques avec la domestication est la disparition de la capacité à disperser chez les graminées en particulier via la perte du rachis cassant empêchant la dispersion des graines (Purugganan & Fuller, 2009; Tanno & Willcox, 2012; Fuller *et al.*, 2014). Les pratiques de récolte par l'utilisation de faucille ou le déracinement des plants auraient conduit à sélectionner uniquement les grains encore fixés au rachis, jusqu'à la fixation progressive de ce trait. La fixation de ce trait ne résulterait pas uniquement de l'utilisation de la faucille car pour certaines civilisations, en Chine par exemple, la faucille est apparue bien après que les premières formes domestiquées se soient établies (Fuller, 2007; Fuller *et al.*, 2010). Un second trait majeur de la domestication est l'augmentation de la taille ou du poids des fruits et des graines. Celui-ci résulterait d'une sélection non-intentionnelle, associée au travail du sol et à la profondeur d'enfouissement des graines (Harlan *et al.*, 1973; Purugganan & Fuller, 2009). Les grosses graines sont plus à même d'émerger efficacement et rapidement et donc d'être avantagées dès le stade de germination et dans leur croissance. Enfin, certaines études ont montré une meilleure résistance à l'herbivorie des ancêtres sauvages comme chez la tomate (Mirnezhad *et al.*, 2010) ou la canneberge (Rodriguez-Saona *et al.*, 2011) comparé à leurs homologues domestiquées. Plusieurs hypothèses ont été envisagées : d'une part, les défenses chimiques chez certaines espèces ont probablement été contre-sélectionnées au cours de la domestication du fait de leur nocivité pour les humains ou le bétail (McKey *et al.*, 2012) ; d'autre part, il est probable que la sélection pour un plus fort rendement des cultures ait entraîné des changements d'allocation des ressources et donc des changements dans le compromis entre croissance et défense (Herms & Mattson, 1992; Rodriguez-Saona *et al.*, 2011; Anten & Vermeulen, 2016).

IV. Des variétés locales aux formes modernes : l'idéotype de Donald du faible compétiteur

Les espèces domestiquées ont connu par la suite une phase d'amélioration ou aussi appelé phase de diversification qui a entraîné de nouveaux changements phénotypiques post-domestication suite à leur diffusion (Meyer & Purugganan, 2013; Abbo *et al.*, 2014b). Cette phase de diversification fait principalement référence à l'adaptation locale des espèces initialement domestiquée à divers agrosystèmes et aux préférences locales, de par leur propagation et leur culture à l'échelle mondiale (Meyer & Purugganan, 2013; Hufford *et al.*, 2019). Ceci mena à des divergences génétiques et phénotypiques entre les populations cultivées générant un large panel de variétés locales aussi connu sous le terme de « landrace » (Chen *et al.*, 2017). Une variété locale constitue donc une population de plantes, cultivée depuis plusieurs générations dans une région donnée, et sur laquelle les agriculteurs ont appliqué une sélection massale⁶ plus ou moins dirigée en ressemant les graines des individus porteurs des caractéristiques morphologiques désirées (Zeven, 1998). Ceci a amené notamment à l'apparition de grains nus enveloppés dans des glumes molles, contribuant fortement à l'amélioration de l'efficacité du battage des grains (Tzarfati *et al.*, 2013). Les variétés locales sont définies par plusieurs auteurs comme des variétés avec un niveau de diversité génétique et phénotypique intra-population élevée, tolérantes à différents stress abiotiques et biotiques, leur permettant de fournir des rendements modestes mais stables entre les années, apportant une source alimentaire sûre pour les communautés locales (Zeven, 1998; Breseghello & Coelho, 2013). La sélection dans les environnements cultivés (perturbé, fertile, compétitif) a favorisé des plantes avec une plus forte biomasse, avec une grande stature, des feuilles larges associées à une acquisition rapide de la lumière (surface foliaire élevée, taux de photosynthèse élevé, forte teneur en azote) et de grosses graines (Milla *et al.*, 2014; Milla & Matesanz, 2017; Roucou *et al.*, 2018; Jones *et al.*, 2021) (Fig. 4). L'évolution des populations cultivées a fini par avoir des conséquences négatives sur leur productivité, liées à l'augmentation en fréquence de phénotypes compétitifs qui surinvestissent dans des structures aériennes et souterraines au détriment de la production de grains, maximisant l'acquisition de ressources et diminuant la quantité de ressources disponibles pour les

⁶ La sélection massale consiste lors de la récolte, à sélectionner les graines issues des plantes les plus performantes ou présentant les caractéristiques désirées, pour le semis suivant (Gallais, 2018).

autres individus de la population (Zhang *et al.*, 1999; Anten & Vermeulen, 2016). En effet, la compétition pour des ressources limitées et partagées favorise dans la plupart des cas les individus ayant une stratégie d'acquisition et d'utilisation des ressources qui maximisent leurs performances individuelles au détriment des performances du groupe, décrivant une situation de Tragédie des Communs (Hardin, 1968 ; Weiner, 2003, 2019). Le concept de la Tragédie des Communs formalise l'idée que, les phénotypes les plus compétitifs dans une population sont amenés à augmenter en fréquence au fil des générations, entraînant une diminution de la performance globale de la population, voire une extinction des populations du fait d'un épuisement des ressources (Hardin, 1968).

Les espèces domestiquées ont été cultivées dans des systèmes de production moderne bien plus denses que les systèmes traditionnels (Postma *et al.*, 2017; Beaugendre *et al.*, 2022). La densité est un facteur majeur qui va conditionner l'intensité de la compétition dans une population, la réponse des plantes aux variations en ressources dues au voisinage et par conséquent leur rendement (Weiner & Freckleton, 2010; Villalobos *et al.*, 2016). L'augmentation de la densité est considérée comme un des facteurs ayant permis l'augmentation des rendements (Khush, 2001), ce qui suggère une meilleure tolérance à la densité des variétés modernes par rapport aux variétés populations. Ceci pourrait en particulier résulter de la sélection de phénotypes permettant de diminuer la compétition entre individus à forte densité. En agronomie, dans les années 1960, l'idée de limiter la compétition intraspécifique pour maximiser les rendements des céréales a été avancée par Donald (1968). Donald dans son approche considère la parcelle comme une communauté, qui grâce à une faible compétition pour les ressources entre les individus du groupe, aura une productivité maximale en peuplement dense. Cette idée s'inscrit dans l'approche de sélection par « idéotype » qui repose sur la sélection de traits associés à l'architecture des plantes (ex. hauteur, orientation et surface des feuilles, nombre de talles). Ces traits sont étroitement liés à l'activité photosynthétique, la croissance, la productivité en grains et la compétition chez les céréales (Donald, 1968; Denison *et al.*, 2003). Ce tournant au cours de la Révolution Verte a conduit à l'émergence de variétés de céréales semi-naines, présentant peu de talles, une rigidité accrue de la tige et des feuilles dressées (Khush, 2001) (Fig. 4). Ces caractéristiques permettent de limiter la compétition intraspécifique pour la lumière dans le peuplement (Donald, 1968). Les changements phénotypiques apportés par cette approche ont permis une meilleure réponse des plantes à l'apport d'engrais, une résistance à

la verse et une meilleure utilisation de la lumière par celles-ci (Evenson & Gollin, 2003; Tian *et al.*, 2021; Niu *et al.*, 2022). Le développement de variétés basées sur l'idéotype du faible compétiteur de Donald, a ainsi permis de contrer l'expression de la tragédie des communs dans les systèmes cultivés en particulier à haute densité (Jennings & De Jesus, 1968; Khalifa & Qualset, 1974; Anten & Vermeulen, 2016). En effet, la sélection artificielle sur certains traits, connus pour être impliqués dans la compétition pour la lumière comme la hauteur des plantes, est allée à l'encontre de la sélection naturelle en favorisant des phénotypes peu compétiteurs pour les ressources, maximisant la productivité du groupe et non plus la productivité de l'individu (Weiner, 2003; Weiner *et al.*, 2010). Ceci pourrait en effet expliquer que les variétés modernes soient plus adaptées à des conditions de forte densité. L'ensemble des améliorations qui impliquent également une meilleure résistance aux stress abiotiques (sécheresse) ou biotiques (maladies, insectes,...) a permis de maximiser la production en peuplement dense (Duvick, 1986) et a conduit à une augmentation substantielle de l'effort reproducteur à la fin du XX^e siècle (Hay, 1995; Gold, 1999). Il est probable que les changements apportés au phénotype aient joué un rôle dans la réponse des individus à leur voisin leur permettant de se maintenir à haute densité (Milla, 2023). En effet, la compétition intraspécifique pour l'accès aux ressources en plus de dépendre de prédispositions phénotypiques (stature, largeur des feuilles, architecture racinaire, ...), dépend aussi de la capacité individuelle à répondre au voisinage (Fig. 5).

| **Les limites de connaissances**

- ❖ La compétition intraspécifique pour les ressources chez les céréales a-t-elle varié au cours de la domestication et de la sélection moderne ?
 - ❖ La réponse à la densité des espèces cultivées a-t-elle varié au cours de la domestication et de la sélection moderne ?
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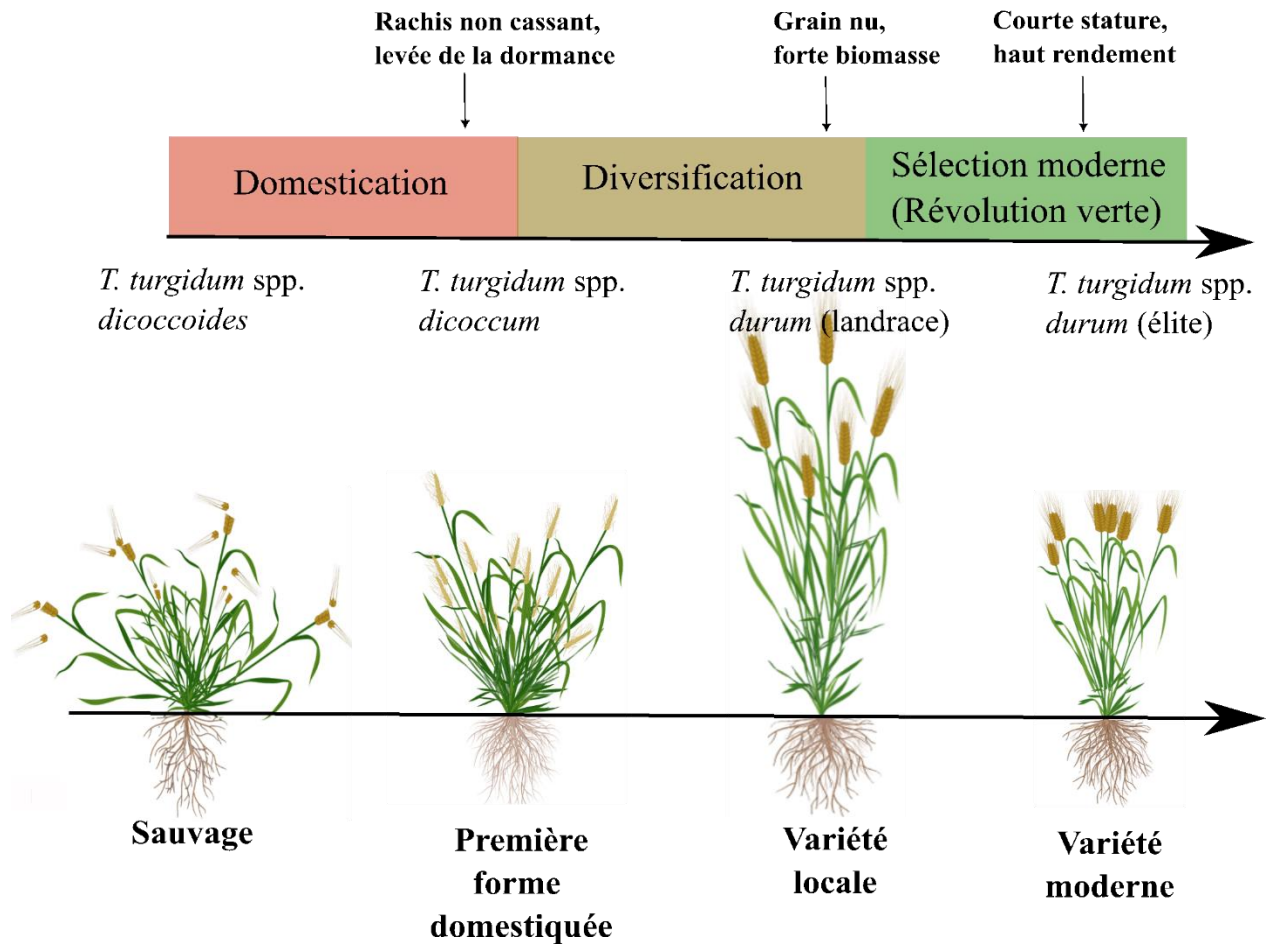


Figure 4. Schéma représentant les principales étapes de l’histoire de domestication et de sélection chez les céréales, en prenant l’exemple du blé tétraploïde. La première forme domestiquée caractérisée notamment par un rachis non cassant (épis qui restent sur les talles), *T. turgidum* spp. *dicoccum*, est apparu il y a 12 000 ans . Puis le blé a connu une étape de diversification qui a amené à des divergences génétiques et phénotypiques entre les populations domestiquées générant un large panel de variétés locales à grain nu, *T. turgidum* spp. *durum* (landrace). Au cours de la Révolution Verte au milieu du XX^{ème} siècle, la sélection moderne a ensuite conduit à des modifications du phénotype comme par exemple à une réduction de la taille des plantes. Les variétés modernes regroupent des génotypes sélectionnés depuis une cinquantaine d’année et sont des variétés à haut rendement *T. turgidum* spp. *durum* (élite). Les dessins sont des interprétations des résultats obtenus durant la thèse. Adapté de Roucou *et al.*, (2018).

V. La compétition pour la ressource dans tous ses états

L'aptitude à la compétition, entre effet et réponse

Les interactions de compétition ont façonné les communautés naturelles, des phénotypes des espèces qui les composent jusqu'à leur structure. L'écologie fonctionnelle comparative a permis un important criblage des traits impliqués dans l'aptitude à la compétition chez les plantes, renforçant le potentiel de l'approche fonctionnelle pour prédire le résultat de la compétition pour les ressources (Keddy & Shipley, 1989; Aarssen, 1989; Keddy, 1992). Cependant, les traits conférant une meilleure aptitude à la compétition ont été longuement débattus en partie dus à des définitions différentes de l'aptitude à la compétition et des mécanismes associés (Grace, 2012). Deux théories se sont longuement opposées, celle de Grime et celle de Tilman (Grime, 1977; Tilman, 1987; Thompson & Grime, 1988). Grime a défini la compétition comme la tendance de deux individus voisins à utiliser le même pool de ressources, amenant un individu à diminuer la valeur sélective de son voisin par la modification de son environnement. Il a alors défini une bonne aptitude à la compétition comme la capacité d'une espèce à s'accaparer rapidement les ressources plutôt que de tolérer un stress en ressource. Ainsi, un individu avec une vitesse rapide de croissance (Relative Growth Rate, RGR) est considéré selon Grime comme le meilleur compétiteur. Tilman quant à lui, a proposé une définition de la compétition davantage centrée sur la tolérance d'un faible niveau de ressources. A partir d'un modèle appliqué cette fois-ci à des populations, Tilman propose que les espèces les plus compétitives sont celles capables d'abaisser plus fortement le pool de ressources et de se maintenir dans ces conditions (Tilman, 1982). Par la suite, Goldberg s'est emparé du débat et a tenté de réconcilier ces deux aspects de la compétition en proposant deux chemins par lesquels un individu peut être un bon compétiteur, soit en diminuant rapidement le niveau de ressources, soit en continuant à croître malgré la baisse de la disponibilité en ressources suite à leur exploitation par d'autres (Goldberg, 1990). Selon Goldberg, l'aptitude à la compétition implique donc ces deux aspects et est défini par la capacité d'un individu à s'accaparer les ressources et réduire la performance de ses voisins aussi appelé « l'effet compétiteur », et par sa capacité à tolérer une diminution du niveau de ressources dû au voisinage, aussi nommé « la réponse à la compétition » (Goldberg & Fleetwood, 1987; Goldberg, 1990) (Fig. 5). En pratique, ces deux composantes sont complexes à discriminer étant toutes deux associées à des traits liés à

la capture et l'utilisation des ressources par les plantes (Goldberg, 1997). En effet, de nombreux traits sont impliqués simultanément dans les deux aspects de la compétition. Par exemple, la hauteur est un trait d'effet compétiteur majeur dans les peuplements (Gaudet & Keddy, 1988; Violle *et al.*, 2009) mais elle constitue aussi un trait de réponse à la compétition pour la lumière (Fig. 5). Une petite plante en compétition avec de plus grandes plantes aura un faible effet compétiteur, car elle captera moins de lumière et ne diminuera pas la quantité de lumière pour ces voisins, mais elle répondra fortement à la compétition en allongeant sa tige en réponse à l'ombrage dû aux plantes voisines (Aphalo *et al.*, 1999). Des approches expérimentales ont permis de dissocier les deux aspects de la compétition et d'identifier des traits d'effet et/ou de réponse à la compétition (Goldberg & Fleetwood, 1987; Violle *et al.*, 2009).

Plasticité, la manipulation de la compétition

La plasticité phénotypique définit le mécanisme par lequel un génotype exprime différents phénotypes dans différents environnements abiotiques et biotiques (Sultan, 2000). A l'échelle d'un individu, on parle de réponse plastique lorsque des modifications de l'environnement entraînent des changements dans les valeurs de trait de l'individu (Bradshaw, 1965). Du fait de leur vie fixée, la plasticité joue un rôle essentiel dans l'adaptation des plantes aux différents environnements qu'elles peuvent rencontrer et peut positivement agir sur la valeur sélective des individus. Nous parlerons alors de plasticité « adaptative ». Un exemple bien décrit de plasticité morphologique et physiologique adaptative est l'élongation de la tige en réponse à l'ombrage dû au voisinage (Ballaré *et al.*, 1990). De plus, la plasticité joue un rôle clé dans les interactions plante-plante puisqu'elle contribue à la variation des valeurs de traits (Bradshaw, 1965) et influence l'acquisition et l'utilisation de ressources par les plantes (Grime & Mackey, 2002) (Fig. 5). En effet, en réponse à la compétition, les plantes peuvent exprimer un phénotype différent, qui si la plasticité est adaptative, permettra une meilleure acquisition des ressources aériennes et souterraines en présence de voisins (Poorter & Lambers, 1986; Sorrensen-Cothorn *et al.*, 1993; Callaway *et al.*, 2003; Crick & Grime, 1987). La plasticité phénotypique peut donc conférer aux plantes une meilleure aptitude à la compétition (Fig. 5). Par exemple, la plasticité phénotypique des racines dans leur croissance et leur distribution, mais aussi dans leur capacité à acquérir des nutriments comme l'azote ou le phosphore, a induit une amélioration de l'aptitude à la compétition des plantes dans les systèmes sauvages comme cultivés (Callaway *et al.*, 2003; De Kroon *et al.*, 2003; Novoplansky, 2009; Liu

et al., 2015). Une étude récente a par ailleurs montré qu'une augmentation de la teneur en silicium du blé dur en réponse à la compétition était couplée à une augmentation de la hauteur des plantes (de Tombeur *et al.*, 2022; Article S2). Le silicium pourrait donc jouer un rôle indirect dans la compétition intraspécifique à travers son influence sur la hauteur des plantes. La plasticité de différents organes en réponse à la compétition pour la lumière tient une place centrale dans l'étude de la compétition intraspécifique (Ballaré *et al.*, 1990; Aphalo *et al.*, 1999; Sultan, 2000), avec en particulier l'étude du « shade-avoidance syndrome » (Smith & Whitelam, 1997).

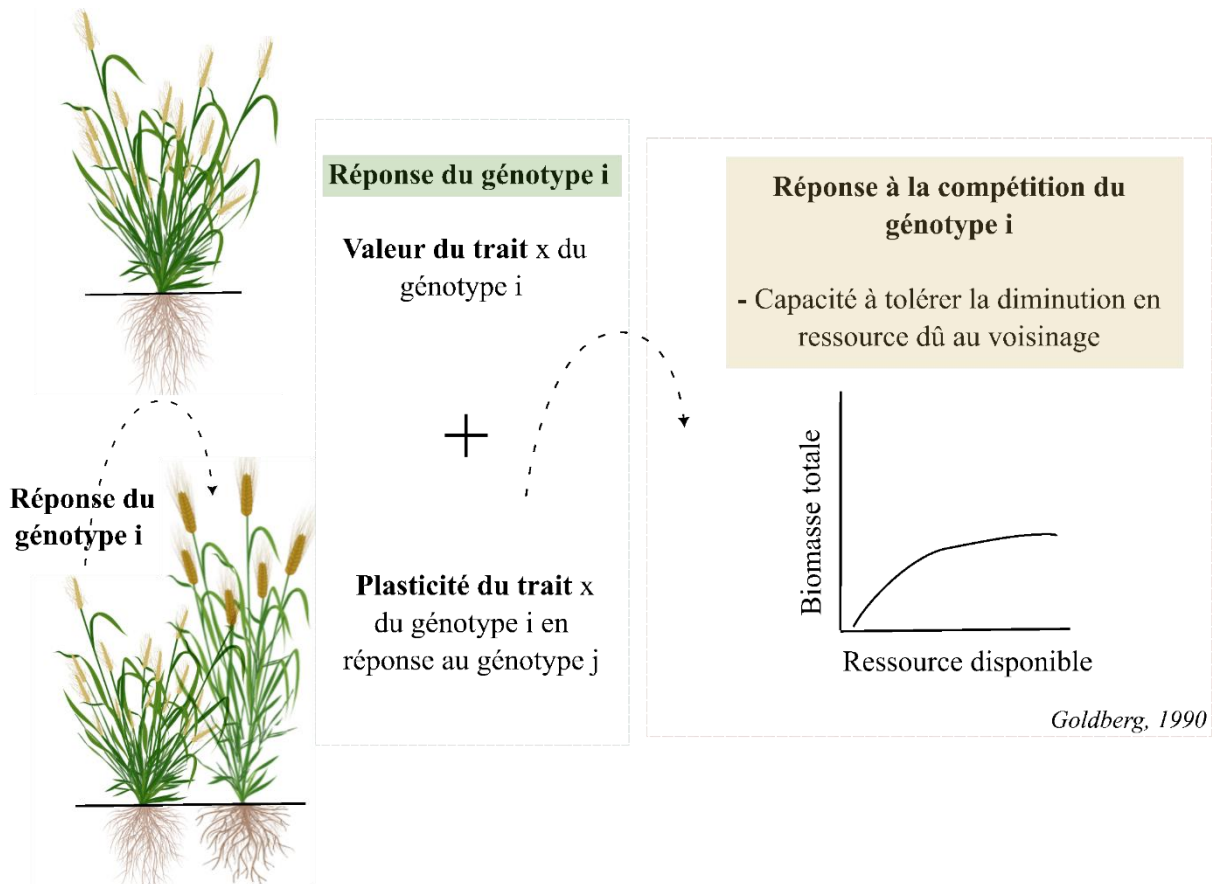


Figure 5. Schéma synthétique illustrant la réponse du génotype i au voisinage du génotype j. La réponse à la compétition est la combinaison de la valeur intrinsèque du génotype i (sa valeur de trait x en condition isolée) et de la plasticité de ce trait x en réponse au voisin j. La combinaison de la valeur intrinsèque et de la plasticité décrit la réponse à la compétition du génotype i qui correspond à sa capacité à tolérer la diminution en ressource due au voisinage. La biomasse totale du génotype i va varier en fonction de la ressource disponible en réponse à la compétition. La biomasse totale peut diminuer plus ou moins fortement en fonction de la capacité du génotype i à tolérer la diminution en ressources disponibles due au génotype j. Adaptée de Goldberg, (1990).

Au-delà de la nature intrinsèque du phénotype, l'intensité de la compétition est également déterminée par la distance phénotypique entre une espèce (ou un génotype) et ses voisins (Goldberg & Landa, 1991). La compétition asymétrique est une composante majeure des interactions plante-plante en particulier pour l'acquisition de la lumière (Freckleton & Watkinson, 2001). En effet, de fortes différences phénotypiques entre des plantes en compétition peuvent se traduire par une relation de « dominance » d'un individu sur un autre (Weiner, 1990). La magnitude de la plasticité exprimé par un génotype dépend ainsi des valeurs de traits de la plante voisine (Abakumova *et al.*, 2016; Turcotte & Levine, 2016). La plasticité peut constituer un moyen pour la plante « désavantagée » de converger vers les valeurs de traits de son voisin (de minimiser les différences phénotypiques) (Vermeulen *et al.*, 2008; Fox & Vasseur, 2008; Carmona *et al.*, 2019). Par exemple, des conditions de peuplement dense peuvent amener à des inégalités de hauteurs au sein de la population créant alors une forte asymétrie dans la compétition et une plus forte plasticité de la hauteur (Xiao *et al.*, 2006).

La plasticité est par ailleurs un mécanisme qui peut également favoriser la coexistence entre espèces ou entre génotypes. En effet, la plasticité peut entraîner une divergence dans les valeurs de traits entre deux espèces, favorisant alors la complémentarité entre les niches écologiques des espèces et le partage des ressources (Ashton *et al.*, 2010; Turcotte & Levine, 2016). Dans les cultures intercalaires d'espèces annuelles, il a par exemple été montré que la plasticité phénotypique de plusieurs traits aériens améliorait la disponibilité de la lumière et contribuait à des effets positifs sur le rendement final (Zhu *et al.*, 2015, 2016). Malgré de nombreuses études sur la plasticité, les causes et les effets de la plasticité sur les interactions plante-plante en particulier dans les systèmes cultivés restent encore peu explorées, rendant sa gestion difficile pour les sélectionneurs menant à une question récurrente : 'Que doit-on faire avec la plasticité ?' Par ailleurs, l'effet de la domestication et de la sélection moderne sur la plasticité phénotypique reste encore peu exploré, notamment par des approches expérimentales, alors que sa place pourrait être centrale dans les interactions de compétition.

L'uniformisation génétique et phénotypique des plantes cultivées, mais aussi des pratiques agricoles (culture monospécifique/monogénotypique, milieu homogène) au cours de l'évolution des cultures pourrait avoir contraint la capacité des espèces domestiquées à répondre aux variations environnementales par plasticité phénotypique (Kebrom & Brutnell, 2007; Grossman & Rice, 2012; Des Marais *et al.*, 2013; Matesanz & Milla, 2018; Milla, 2023). Chez le blé, une récente

étude suggère que la sélection de plantes courtes au cours de la Révolution Verte a diminué la plasticité en hauteur chez les variétés modernes, les rendant moins plastique à l'ombrage et donc moins sensible à la présence d'un voisin (Colombo *et al.*, 2022). Cependant, dans l'état actuel des connaissances, il est difficile de parler d'une perte généralisée de plasticité chez les espèces domestiquées, car selon les traits étudiés, les espèces considérées ou encore les conditions environnementales testées, il n'existe pas toujours de différences de plasticité avec les progéniteurs sauvages (Matesanz & Milla, 2018; Hufford *et al.*, 2019).

La compétition est médiée par la densité

La biomasse totale des plantes par unité de surface dépend de la densité de plantes présentes. En effet, il existe un lien étroit entre compétition et densité de la population (Weiner & Freckleton, 2010). Dans une population, la disponibilité en ressources varie dans le temps et l'espace, ce qui peut limiter la croissance individuelle et provoquer une situation de compétition entre les plantes voisines (Villalobos *et al.*, 2016). Il a été montré que la biomasse totale des plantes par unité de surface était proportionnelle à la densité aux premiers stades de développement. Cette proportionnalité diminue avec l'augmentation de la densité et conduit généralement à une phase où la biomasse totale des plantes par unité de surface est indépendante de la densité (Bleasdale, 1966) (Fig. 6). En fait, à haute densité, la croissance individuelle des plantes est fortement limitée par la compétition individuelle pour les ressources, ce qui se traduit par un rendement maximal constant quelle que soit la densité (« rendement final constant »; Weiner & Freckleton, 2010) (Fig. 6). L'ajout de plantes n'augmente donc plus le rendement. À des densités encore plus élevées, le risque de mourir de certains individus avant reproduction augmente, entraînant un « self-thinning » ou « auto-éclaircissement » dans la population (Westoby, 1984) (Fig. 6). Ainsi, plus la densité initiale est élevée, plus tôt et plus forte est la compétition pour les ressources et plus rapidement est atteint ce plateau. La réponse à la densité des cultures est donc une question majeure pour le rendement (Deng *et al.*, 2012a,b), notamment en raison du lien étroit entre biomasse totale et effort reproducteur (Weiner *et al.*, 2009; Villalobos *et al.*, 2016). En effet, les ressources étant limitées, la réduction de la biomasse végétative moyenne individuelle en réponse à la densité entraîne une diminution de la part de la biomasse totale allouée aux structures reproductives (Weiner *et al.*, 2009). En réponse à la densité, la biomasse reproductrice augmente proportionnellement jusqu'à atteindre un rendement maximal constant. En surpeuplement, le rendement récoltable (en grains)

peut diminuer (forme parabolique de la relation rendement-densité) en raison de la verse ou de maladies mais aussi à cause de changement dans l'allocation des ressources (Beaugendre *et al.*, 2022). En fait, certains individus en réponse au surpeuplement seront en dessous de leur biomasse minimale pour se reproduire, entraînant une diminution de la biomasse reproductive avec la densité (Weiner, 1990).

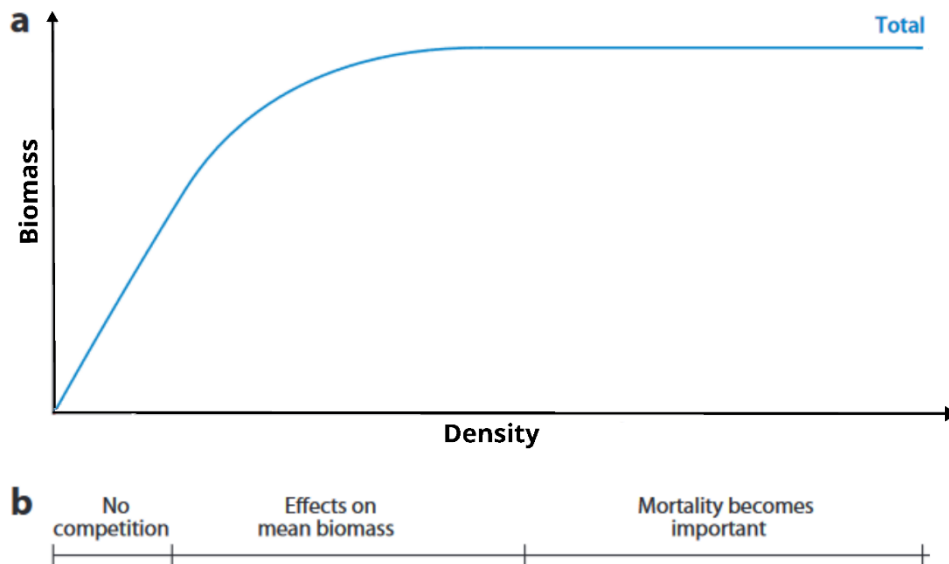


Figure 6. a) Réponse à la densité de la biomasse totale du peuplement conduisant à un rendement final constant quelle que soit la densité. b) Effet de la compétition sur la biomasse conduisant à une forte mortalité dans le peuplement. Tirée de Weiner & Freckleton, (2010).

| Les limites de connaissances

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- ❖ Comment la plasticité des traits en réponse à la compétition a varié au cours de la domestication et de la sélection moderne ?
 - ❖ Comment a évolué la plasticité adaptative chez les espèces cultivées ?
 - ❖ Le rendement final constant a-t-il été modulé au cours de la domestication et de la sélection moderne ?
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VI. Maintien des compromis à l'échelle intraspécifique ?

Il est maintenant reconnu que les traits fonctionnels varient au sein d'une espèce et que la variation intraspécifique influence drastiquement la réponse des espèces et l'effet qu'elles peuvent avoir sur leur environnement (Cianciaruso *et al.*, 2009; Jung *et al.*, 2010; Bolnick *et al.*, 2011; Violle *et al.*, 2012). L'utilisation d'une seule valeur de trait, comme une moyenne, pour décrire une espèce donnée peut donc masquer une grande variation fonctionnelle au sein d'une population (Bolnick *et al.*, 2011) ou entre des populations le long de gradients environnementaux (Albert *et al.*, 2010). Bien que la variabilité intraspécifique soit désormais davantage considérée, elle n'a que récemment été prise en compte dans l'exploration de la variation phénotypique chez les plantes. Ainsi, une incertitude demeure quant au maintien au niveau intraspécifique, des compromis écophysologiques décrits au niveau interspécifique (Laforest-Lapointe *et al.*, 2014). En effet, on peut s'attendre à des changements dans les relations entre traits entre ces deux échelles, en raison de l'adaptation locale des espèces (écotypes) et de leur plasticité phénotypique en réponse à des facteurs environnementaux (Wright & Sutton-Grier, 2012; Niinemets, 2015; Anderegg *et al.*, 2018). Des études récentes ont montré que les compromis foliaires d'acquisition-conservation des ressources (LES) décrits à l'échelle interspécifique pouvaient se maintenir au niveau intraspécifique (Albert *et al.*, 2011; Vasseur *et al.*, 2012; Sartori *et al.*, 2019; Fajardo & Siefert, 2018). L'intégration de la variabilité fonctionnelle intraspécifique pouvait en outre modifier le positionnement des espèces le long des axes de variation et produisait un continuum fonctionnel plutôt que des groupes clairs d'espèces (Albert *et al.*, 2011). L'étude de Hu *et al.*, (2015) a identifié des covariations de traits similaires à l'échelle intraspécifique et à trois échelles spatiales différentes suggérant que la variation intraspécifique principalement expliquée par des différences climatiques et pédologiques était contrainte par les mêmes compromis. Ces résultats suggèrent malgré tout de fortes contraintes écophysologiques et biophysiques sur les valeurs de traits et leur expression (Reich *et al.*, 1997; Shoval *et al.*, 2012; Garland *et al.*, 2022).

VII. Les contraintes allométriques

De nombreux traits associés à l'allocation de la biomasse ou encore au métabolisme varient avec la taille des organismes à travers les taxons (Schmidt-Nielsen, 1984; Niklas, 2004). En effet, un

important corpus théorique s'accorde à dire que la quantité de graines produites dépendrait de la biomasse atteinte par la plante (Weiner *et al.*, 2009; Bonser & Aarssen, 2009). Chez les plantes, le premier axe de la variation phénotypique est d'ailleurs majoritairement expliqué par la taille de la plante entière et de ses graines (Díaz *et al.*, 2016). De nombreuses études se sont ainsi attachées à étudier les relations trait-taille et ont démontré que les traits variaient de manière non-proportionnelle avec la taille, résultant en une relation non-linéaire, mieux connue sous le terme de « relation allométrique » (Huxley, 1924; Gould, 1966). Les travaux de Brody et Kleiber révélant une pente de 3/4 entre le taux métabolique et la taille du corps des animaux (Kleiber, 1947; Brody & Lardy, 1946 dans Niklas, 2004), ont amené à supposer que les relations trait-taille étaient en fait contraintes par des lois biophysiques et biomécaniques (West & Brown, 2005). Ainsi, l'observation d'une constance dans les coefficients allométriques à travers de multiples échelles d'organisation biologique et de taxons ont amené au développement de grandes théories mécanistes, avec notamment la Metabolic Scaling Theory (MST), décrivant les premiers principes de l'allométrie chez les plantes (West *et al.*, 1997, 1999; Enquist *et al.*, 1999). Ces contraintes physiques sont décrites par Taylor & Thomas, (2014) comme « celles qui définissent l'espace que l'évolution et le comportement sont libres d'explorer ». Les contraintes physiques entre les traits constituent donc des limites pour la variation phénotypique et son évolution (Garland *et al.*, 2022). Certaines études ont cependant montré une variation forte des coefficients allométriques entre les espèces sauvages (Poorter *et al.*, 2015) et au sein des espèces (Vasseur *et al.*, 2018) suggérant que l'allométrie pourrait être expliquée, par d'autres contraintes que les seules lois biophysiques, notamment par des processus écologiques et évolutifs tels que la sélection naturelle (Glazier, 2022).

VIII. Compromis et contraintes au sein d'une espèce cultivée ?

Une question persiste dans la littérature sur l'effet de la domestication et de la sélection artificielle sur la structure de la variation phénotypique au sein des espèces cultivées et le maintien des compromis observés au niveau interspécifique. En effet, l'effet conjoint de la sélection naturelle et artificielle au cours de la domestication et de la sélection moderne est susceptible d'avoir influencé la gamme de variation des traits fonctionnels et conduit à des changements dans les covariations

entre traits chez les espèces cultivées (Milla *et al.*, 2014, 2015; Cantarel *et al.*, 2020). On pourrait s'attendre à des corrélations plus fortes ou nouvelles, entre certains traits sélectionnés ou au contraire des liens affaiblis entre les traits (Milla *et al.*, 2014). Une étude a en particulier montré qu'il y avait plus de corrélations entre le compartiment aérien et racinaire pour le compartiment sauvage du blé dur suggérant que la sélection aurait pu découpler les stratégies d'acquisition et d'utilisation des ressources entre les différents organes (Roucou *et al.*, 2018). Au contraire, Martín-Robles *et al.*, (2019) ont révélé que l'évolution vers de grandes plantes au cours de la domestication a impliqué une évolution corrélée de racines plus épaisses. De plus, la diminution de la variation sur certains traits ciblés par la sélection moderne a pu entraîner des changements dans la structuration de la variation phénotypique. En effet, ces traits, qui chez les espèces sauvages expliquaient une grande partie de la variation, pourraient ne plus structurer les axes de variation majeurs décrits au niveau interspécifique. Il est aussi probable que la sélection artificielle ait imposé une forte pression sur les contraintes d'allocation de biomasse au sein de la plante en modifiant les relations allométriques trait-taille au sein des espèces cultivées. Un exemple portant sur la comparaison des progéniteurs sauvages et des variétés modernes chez la papaye a montré des changements dans la relation allométrique entre le diamètre de la tige et la hauteur des plantes (Niklas & Marler, 2007). Cependant, à quel point l'évolution des cultures a affaibli, renforcé ou modulé les compromis fonctionnels et les contraintes allométriques est une question encore peu explorée. Pourtant, les contraintes fonctionnelles et structurelles constituent une limite importante pour l'amélioration des cultures et les outrepasser peut constituer un moyen d'adapter les cultures au défi de production à venir (Denison *et al.*, 2003; Denison, 2015).

| Les limites de connaissances

- ❖ Les pressions de sélection associées à la domestication et à l'amélioration variétale ont-elles eu un effet sur la structuration de la variation phénotypique des espèces cultivées ?
 - ❖ La sélection artificielle a-t-elle permis de sortir des contraintes allométriques classiquement observées chez les espèces sauvages ?
 - ❖ Est-ce que l'intégration de la variation intraspécifique entraînerait des changements dans la structure de la variation phénotypique chez les plantes ?
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IX. Objectifs de la thèse

Dans ce contexte, étudier les changements passés et récents du phénotype des espèces cultivées, par une approche comparative en écologie fonctionnelle, peut permettre d'appréhender les stratégies écologiques des espèces cultivées et de comprendre la performance des cultures. L'objectif général de cette thèse est d'évaluer comment le phénotype et les stratégies écologiques d'une espèce cultivée ont varié au cours de la domestication et de la sélection moderne et d'analyser les conséquences de ces changements phénotypiques sur les interactions de compétition intraspécifique, un processus majeur pour l'amélioration du rendement et pour la diversification des cultures (Fig. 7).

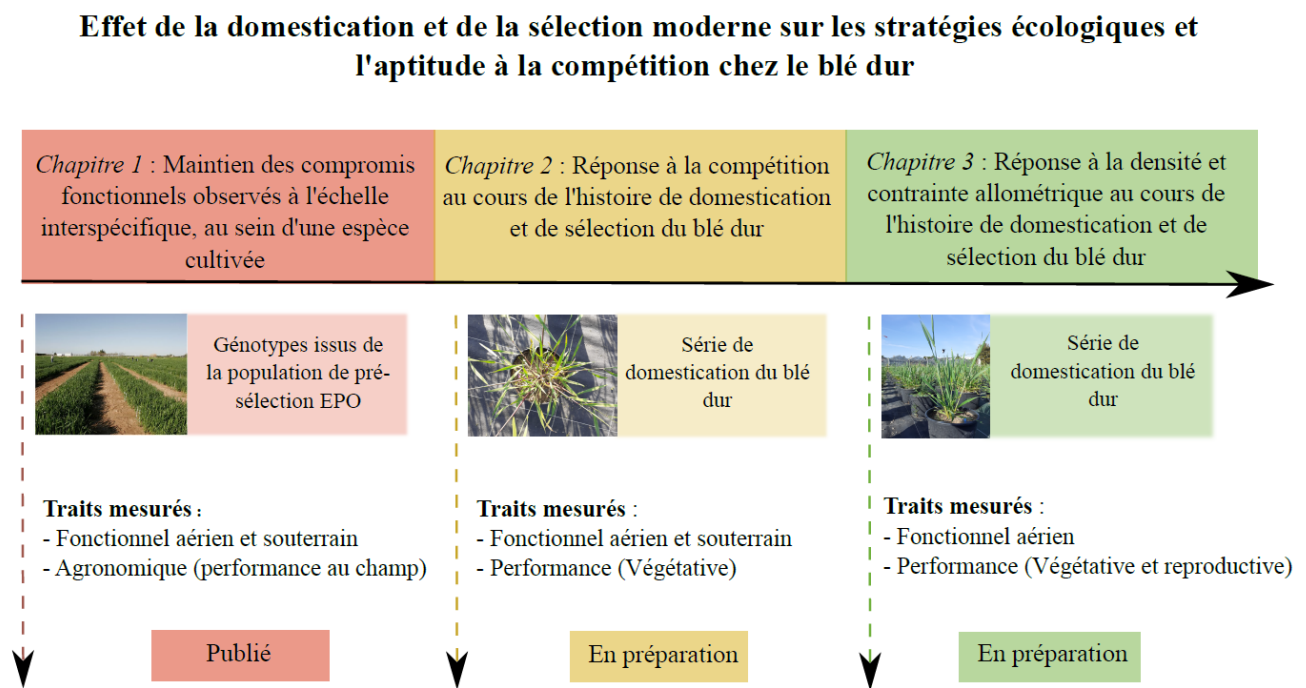


Figure 7. Représentation schématique des chapitres, de l'objectif général de la thèse, et du statut des articles associés.

Les questions spécifiques de ma thèse sont :

- (1) La sélection artificielle a-t-elle entraîné des changements dans les compromis fonctionnels observés au niveau interspécifique ? Les traits fonctionnels expliquent-ils la performance agronomique au champ ?

Dans ce chapitre, à l'aide de données issues d'une expérimentation au champ, nous testons si des compromis fonctionnels observés au niveau interspécifique sont maintenus au sein d'une espèce cultivée. Nous avons également cherché à évaluer quels traits ou combinaisons de traits pouvaient expliquer la variation de la performance agronomique du blé dur.

- (2) Comment le phénotype et la réponse à la compétition ont-ils été modulés au cours de la domestication et de la sélection moderne ? La plasticité en réponse à la compétition a-t-elle varié avec la domestication et la sélection moderne ?

Dans cette partie, à partir d'un panel de génotypes issu de la série de domestication du blé dur, nous avons cherché à tester si la domestication et la sélection moderne avaient impacté le phénotype et la réponse des traits des plantes à la compétition. Nous avons également cherché à décortiquer quel aspect du phénotype, la valeur intrinsèque (trait condition isolé), la valeur du trait en réponse à la compétition ou la plasticité du trait, expliquait le mieux la performance des génotypes en compétition.

- (3) La domestication et la sélection ont-elles entraîné des changements dans la réponse des cultures à la densité et dans les relations allométriques ?

Pour répondre à cette dernière question, nous avons cherché à tester, à partir d'une série de domestication chez le blé dur, si la réponse des traits à la densité variait au cours de la domestication et de la sélection moderne. Nous avons également cherché à évaluer comment les patrons d'allocation de la biomasse variaient entre les différents compartiments génétiques représentatifs des étapes clé de la domestication et de la sélection moderne du blé dur.

X. Une approche fonctionnelle et expérimentale sur le blé dur

Pour répondre à ces problématiques, nous avons combiné une approche fonctionnelle et expérimentale. Nous avons utilisé le blé dur ou *Triticum turgidum*, espèce domestiquée au Moyen-Orient, pour laquelle l’histoire de domestication et de sélection est bien documentée. Le blé dur est la 10^e céréale la plus importante et la plus couramment cultivée dans le monde, avec une production totale mondiale d’environ 40 millions de tonnes par an (Beres *et al.*, 2020; Xynias *et al.*, 2020; International Grains Council). Les pays du bassin méditerranéen (Algérie, Turquie, Italie, Maroc, Syrie, Tunisie, France, Espagne et Grèce) englobent environ 50 % de la superficie et de la production mondiale du blé dur (Tedone *et al.*, 2017). Les autres pays de production de blé dur sont le Canada, le Mexique, les États-Unis, la Russie, le Kazakhstan, l’Australie et l’Inde. Le blé dur est principalement impliqué dans la fabrication des pâtes, mais constitue également un ingrédient important du couscous et du boulgour.

Matériel biologique et données

Dans le cadre du premier chapitre, nous avons utilisé des données mesurées au champ sur 179 lignées fixées de blé dur issues d’une population de pré-sélection (EPO) développée par l’INRAE de Montpellier. EPO est une population composite génétiquement diversifiée, fondée à partir de sous-espèces de blé, sauvage, primitive et moderne (David *et al.*, 2014). Dans l’ensemble, EPO a été sélectionnée pour capturer une forte proportion de la variabilité phénotypique de la sous-espèce *Triticum turgidum*. En pratique, pendant une dizaine d’années, des graines ont été collectées à la fois sur des plantes stériles allofécondées (20 %) et sur des plantes hermaphrodites autofécondées (80 %), puis regroupées pour constituer la génération suivante. Puis, 500 épis ont été choisis et ont subi cinq générations d’autofécondation pour obtenir des lignées fixées. Sur la base de données génotypiques, 180 lignées fixées ont été sélectionnées pour constituer une collection de base englobant la majeure partie de la variabilité génétique présente dans les 500 lignées d’origine (Montazeaud *et al.*, 2020). Le chapitre 1 s’appuie sur les données de traits fonctionnels et de performance collectées au champ durant la thèse de Germain Montazeaud, dans l’expérimentation décrite dans Montazeaud *et al.*, (2020). Nous avons également utilisé des données génétiques disponibles pour ces lignées EPO, obtenues à partir d’une méthode de génotypage à haut débit

utilisant la puce TaBW280K comprenant 420 000 SNP (« Single Nucleotide Polymorphisms ») répartis le long du génome (David *et al.*, 2014; Rimbart *et al.*, 2018).

Table 1. Traits fonctionnels et de performance mesurés dans le cadre des expériences de la thèse.

Traits mesurés	Unité	Chapitre
Aérien		
Vegetative height (Height/plant height)	cm	1, 2, 3
Specific leaf area (SLA)	m ² .kg ⁻¹	2
Leaf mass area (LMA)	kg.m ⁻²	1
Leaf area (LA)	cm ²	2
Leaf dry matter content (LDMC)	mg.g ⁻¹	2
Leaf nitrogen content (LNC)	%	1
Heading date	°days	1, 3
Racinaire		
Specific root length (SRL)	m.g ⁻¹	1, 2
Root length density (RLD)	cm.cm ⁻³	1
Root diameter (RD)	mm	1, 2
Root tissue density (RTD)	g.cm ⁻³	1, 2
Root branching intensity (RBI)	number of tips per length unit	1, 2
Root angle (RA)	°	1
Root: shoot ratio		2
Performance		
Number tillers		2, 3
Vegetative biomass/Aerial biomass	g	2, 3
Biomass yield (BY)	g.m ⁻²	1
Root biomass	g	2
Spike biomass (Reproductive biomass)	g	3
Grain yield (GY)	g.m ⁻²	1
Harvest index		1
Seed number	Seed number per m ²	1
Thousand kernel weight (TKW)	g	1

Dans les deuxième et troisième chapitres, nous avons utilisé une série de domestication (Fig. 4 & Fig. 8), constitué de 40 génotypes de blé dur, répartis de manière équilibrée dans quatre compartiments génétiques représentatifs de l'histoire de domestication et de sélection moderne du blé dur : le blé sauvage (*T. turgidum dicoccoides*), la première forme domestiquée (*T. turgidum dicoccum*) et le blé dur (*T. turgidum durum*). Ce dernier groupe a ensuite été divisé en deux sous-groupes, selon les périodes pré- et post-révolution verte (depuis années 1970 à 1990). Les graines ont été fournies par l'INRAE de Montpellier et proviennent initialement de différentes collections internationales.



Figure 8. Photographies illustrant la série de domestication du blé dur, respectivement : *T. turgidum dicoccoides* (DD), *T. turgidum dicoccum* (DC), *T. turgidum durum* Landrace (DL), *T. turgidum durum* élite (DE).

Approche expérimentale en pot

Pour répondre aux questions du chapitre 2 et 3, nous avons réalisé deux expérimentations à l'extérieur dans des pots sur le terrain expérimental du CEFE (Fig. 9 & Fig. 10 & Encadré 3). Les plantes dans ces deux expérimentations ont été arrosées manuellement 2 à 3 fois par semaine (~3h par arrosage) et plusieurs apports d'engrais (azote, potassium et phosphore) ont été effectués au cours de l'expérience. Les adventices ont été contrôlées par arrachage manuelle. L'expérimentation en pot bien qu'elle soit peu représentative des conditions réelles de culture a pour avantage de

placer les géotypes dans les mêmes conditions de sol, de nutriments et d'eau. Elle permet donc de mieux contrôler la variation environnementale par l'intermédiaire d'un dispositif en bloc et de mesurer des plus facilement des traits sur les mêmes individus placés dans les mêmes conditions de croissance. La taille du pot constitue également une contrainte sur la croissance du système racinaire et donc sur les valeurs de traits et les potentielles stratégies racinaires (Freschet *et al.*, 2021). Le sol utilisé était un substrat local sablo-argilo-calcaire qui provenait du terrain expérimental du CEFÉ et qui a été enrichi avec du terreau. Le sol était relativement dense, ce qui a quand même permis de ralentir la croissance des racines, de sorte à ce qu'elles atteignent le fond du pot moins rapidement.

L'expérience impliquée dans le chapitre 2 dont le but était de tester la réponse à la compétition au cours de la domestication et de la sélection moderne est basée sur une approche « phytomètre » ou « cible » (Violle *et al.*, 2009). Cette approche est une approche classique en écologie permettant d'étudier expérimentalement les relations entre traits et aptitude à la compétition, en créant des « associations artificielles » (Goldberg & Fleetwood, 1987; Gaudet & Keddy, 1988). Les géotypes « cible » choisis sont placés au centre d'un pot et entourés par une densité fixe de voisin pour ne pas qu'il y ait d'effet confondant avec la densité (Fig. 9). Le géotype voisin choisi était un géotype de blé dur différents des 40 géotypes cibles sélectionnés. Il s'agissait d'un géotype avec une grande stature et une phénologie précoce, présentant donc de bonnes dispositions phénotypiques pour être un redoutable compétiteur. La performance de la cible est mesurée et comparée entre la condition isolée et la condition en présence de voisins. Il est fait l'hypothèse que les cibles étant isolées au milieu du peuplement n'auront pas d'effet compétiteur sur leurs voisins. Grâce à ce dispositif, la réponse à la compétition est mesurée sur la cible et l'effet compétiteur sur les voisins. Les traits fonctionnels et de performance mesurés sur la cible vont ainsi capturer la réponse de la plante à la diminution de la disponibilité en ressources dû au voisinage.

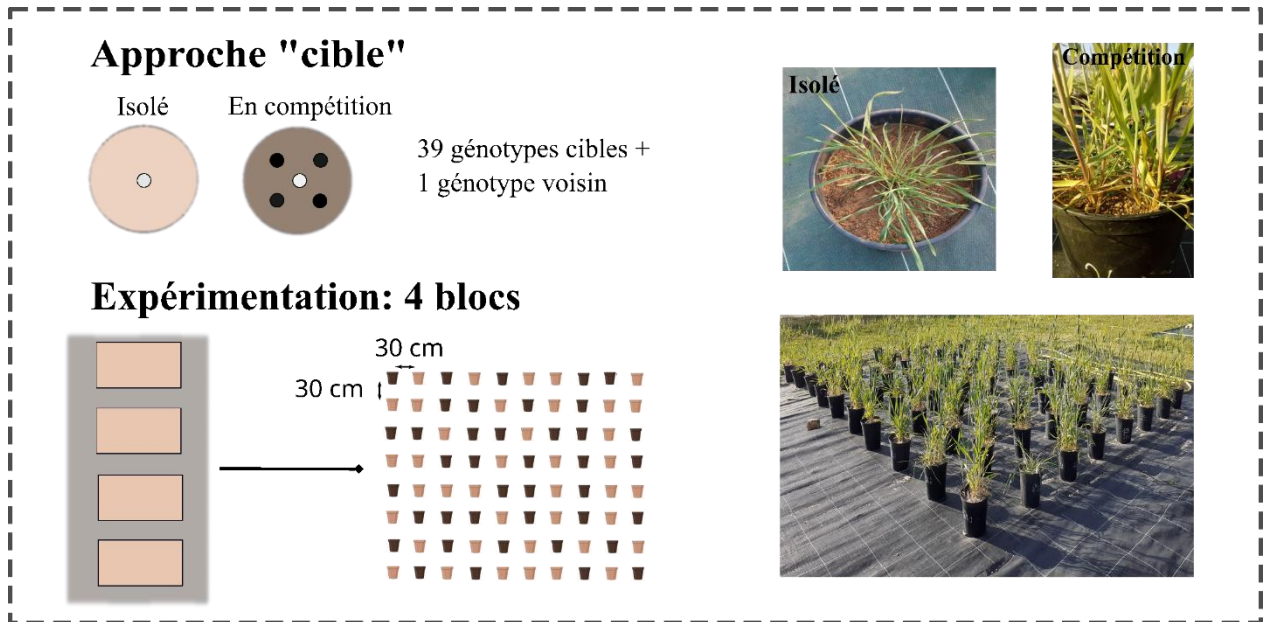


Figure 9. Approche « cible » pour tester la réponse à la compétition au cours de la domestication et de la sélection moderne du blé dur.

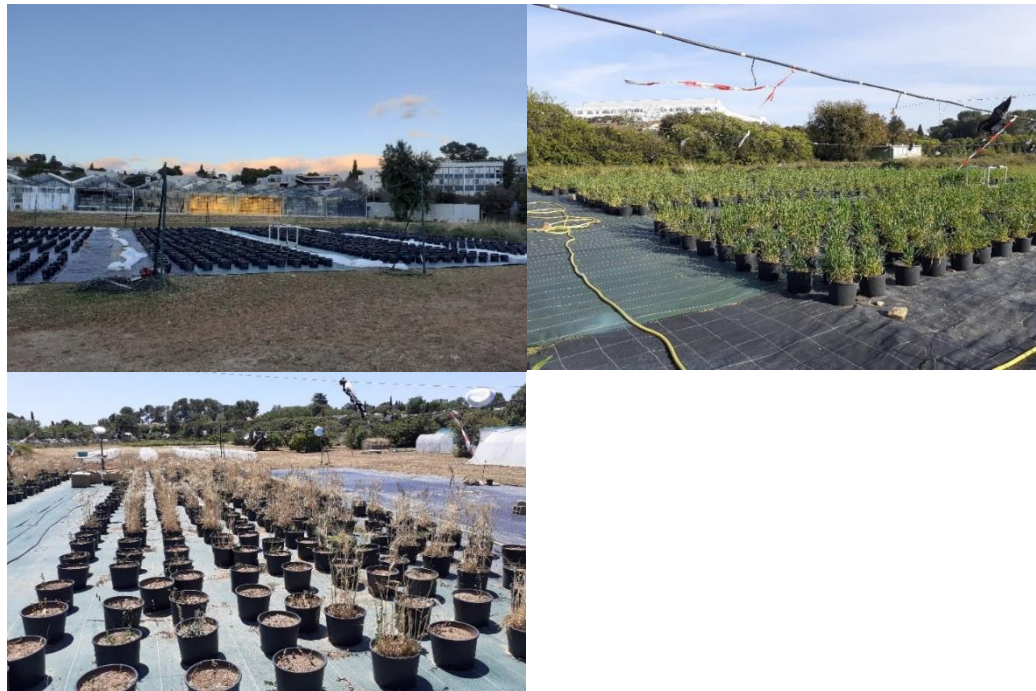


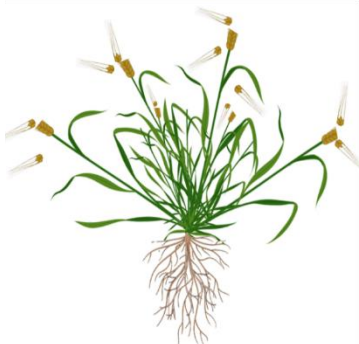
Figure 10. Dispositif expérimental pour tester la réponse à la densité au cours de la domestication et de la sélection moderne du blé dur.

Encadré 3 : Anecdotes, les aléas du terrain



La gourmandise des oiseaux

Au début de l'expérience sur la réponse à la densité, les pies se sont attaquées à nos plantules, constituant un mets de qualité en plein hiver. La crise a été gérée en installant des assiettes en aluminium et de la rubalise, une expérience très décorée.



Blé sauvage, blé volage

C'est en cultivant du blé sauvage que l'on se rend compte que la sélection a bien fait son travail. La dispersion des épis de blé sauvage, une fois mure, nous a donné du fil à retordre. A l'image des premiers agriculteurs, nous avons mené une récolte quotidienne pour s'assurer de collecter le maximum de la biomasse reproductrice des génotypes sauvages.



La cigale et les fourmis

Une petite mésaventure avec des fourmis granivores, *Messor barbarus*, qui volaient les graines qui tombaient au pied des pots. Terre de diatomée ou fortement arrosées, rien n'y faisait, les fourmis volaient.

XI. Bibliographie

- Aarssen LW. 1989.** Competitive Ability and Species Coexistence: A ‘Plant’s-Eye’ View. *Oikos* **56**: 386.
- Abakumova M, Zobel K, Lepik A, Semchenko M. 2016.** Plasticity in plant functional traits is shaped by variability in neighbourhood species composition. *New Phytologist* **211**: 455–463.
- Abbo S, Gopher A, Rubin B, Lev-Yadun S. 2005.** On the Origin of Near Eastern Founder Crops and the ‘Dump-heap Hypothesis’. *Genetic Resources and Crop Evolution* **52**: 491–495.
- Abbo S, Lev-Yadun S, Gopher A. 2014a.** The ‘Human Mind’ as a common denominator in plant domestication. *Journal of Experimental Botany* **65**: 1917–1920.
- Abbo S, Pinhasi van-Oss R, Gopher A, Saranga Y, Ofner I, Peleg Z. 2014b.** Plant domestication versus crop evolution: a conceptual framework for cereals and grain legumes. *Trends in Plant Science* **19**: 351–360.
- Ajal J, Kiær LP, Pakeman RJ, Scherber C, Weih M. 2022.** Intercropping drives plant phenotypic plasticity and changes in functional trait space. *Basic and Applied Ecology* **61**: 41–52.
- Albert CH, Grassein F, Schurr FM, Vieilledent G, Violle C. 2011.** When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics* **13**: 217–225.
- Albert CH, Thuiller W, Yoccoz NG, Soudant A, Boucher F, Saccone P, Lavorel S. 2010.** Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology* **98**: 604–613.
- Altieri MA. 1989.** Agroecology: A New Research and Development Paradigm for World Agriculture. *Agriculture, Ecosystems & Environment* **27**: 37–46.
- Anderegg LDL, Berner LT, Badgley G, Sethi ML, Law BE, HilleRisLambers J. 2018.** Within-species patterns challenge our understanding of the leaf economics spectrum. *Ecology Letters* **21**: 734–744.
- Anten NPR, Vermeulen PJ. 2016.** Tragedies and Crops: Understanding Natural Selection To Improve Cropping Systems. *Trends in Ecology & Evolution* **31**: 429–439.
- Aphalo PJ, Ballare CL, Scopel AL. 1999.** Plant–plant signalling, the shade-avoidance response and competition. *Journal of Experimental Botany* **50**: 1629–1634.
- Araus JL, Ferrio JP, Voltas J, Aguilera M, Buxó R. 2014.** Agronomic conditions and crop evolution in ancient Near East agriculture. *Nature Communications* **5**: 3953.
- Ashton IW, Miller AE, Bowman WD, Suding KN. 2010.** Niche complementarity due to plasticity in resource use: plant partitioning of chemical N forms. *Ecology* **91**: 3252–3260.
- Ballaré CL, Scopel AL, Sánchez RA. 1990.** Far-Red Radiation Reflected from Adjacent Leaves: An Early Signal of Competition in Plant Canopies. *Science* **247**: 329–332.

- Barai K, Calderwood L, Wallhead M, Vanhanen H, Hall B, Drummond F, Zhang Y-J. 2022.** High Variation in Yield among Wild Blueberry Genotypes: Can Yield Be Predicted by Leaf and Stem Functional Traits? *Agronomy* **12**: 617.
- Barot S, Allard V, Cantarel A, Enjalbert J, Gauffreteau A, Goldringer I, Lata J-C, Le Roux X, Niboyet A, Porcher E. 2017.** Designing mixtures of varieties for multifunctional agriculture with the help of ecology. A review. *Agronomy for Sustainable Development* **37**: 13.
- Beaugendre A, Mingeot D, Visser M. 2022.** Complex plant interactions in heterogeneous material require the ecological rethinking of sowing density recommendations for bread wheat. A review. *Agronomy for Sustainable Development* **42**: 9.
- Beres BL, Rahmani E, Clarke JM, Grassini P, Pozniak CJ, Geddes CM, Porker KD, May WE, Ransom JK. 2020.** A Systematic Review of Durum Wheat: Enhancing Production Systems by Exploring Genotype, Environment, and Management ($G \times E \times M$) Synergies. *Frontiers in Plant Science* **11**: 568657.
- Bergmann J, Weigelt A. 2020.** The fungal collaboration gradient dominates the root economics space in plants. *Science Advances* **6**: 37–56.
- Bleasdale JKA. 1966.** Plant growth and crop yield: The fourth Barnes Memorial Lecture. *Annals of Applied Biology* **57**: 173–182.
- Bloom AJ, Chapin FS, Mooney HA. 1985.** Resource Limitation in Plants-An Economic Analogy. *Annual Review of Ecology and Systematics* **16**: 363–392.
- Bogaard A. 2005.** ‘Garden agriculture’ and the nature of early farming in Europe and the Near East. *World Archaeology* **37**: 177–196.
- Bogaard A, Fraser R, Heaton THE, Wallace M, Vaiglova P, Charles M, Jones G, Evershed RP, Styring AK, Andersen NH, et al. 2013.** Crop manuring and intensive land management by Europe’s first farmers. *Proceedings of the National Academy of Sciences* **110**: 12589–12594.
- Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur D. 2011.** Why intraspecific trait variation matters in community ecology. *Trends in ecology & evolution* **26**: 183–192.
- Bonser SP, Aarssen LW. 2009.** Interpreting reproductive allometry: Individual strategies of allocation explain size-dependent reproduction in plant populations. *Perspectives in Plant Ecology, Evolution and Systematics* **11**: 31–40.
- Bourke PM, Evers JB, Bijma P, van Apeldoorn DF, Smulders MJM, Kuyper TW, Mommer L, Bonnema G. 2021.** Breeding Beyond Monoculture: Putting the “Intercrop” Into Crops. *Frontiers in Plant Science* **12**.
- Bradshaw AD. 1965.** Evolutionary Significance of Phenotypic Plasticity in Plants. In: Caspari EW, Thoday JM, eds. *Advances in Genetics*. Academic Press, 115–155.
- Breseghele F, Coelho ASG. 2013.** Traditional and Modern Plant Breeding Methods with Examples in Rice (*Oryza sativa* L.). *Journal of Agricultural and Food Chemistry* **61**: 8277–8286.

- Brisson N, Gate P, Gouache D, Charmet G, Oury F-X, Huard F. 2010.** Why are wheat yields stagnating in Europe? A comprehensive data analysis for France. *Field Crops Research* **119**: 201–212.
- Brody S, Lardy HA. 1946.** Bioenergetics and Growth. *The Journal of Physical Chemistry* **50**: 168–169.
- Bulman P, Hunt LA. 1988.** Relationships among tillering, spike number and grain yield in winter wheat (*Triticum aestivum* L.) in Ontario. *Canadian Journal of Plant Science* **68**: 583–596.
- Callaway RM, Pennings SC, Richards CL. 2003.** Phenotypic Plasticity and Interactions Among Plants. *Ecology* **84**: 1115–1128.
- Cantarel AAM, Allard V, Andrieu B, Barot S, Enjalbert J, Gervais J, Goldringer I, Pommier T, Saint-Jean S, Le Roux X. 2020.** Plant functional trait variability and trait syndromes among wheat varieties: the footprint of artificial selection. *Journal of Experimental Botany* **72**: 1166–1180.
- Carmona CP, de Bello F, Azcárate FM, Mason NWH, Peco B. 2019.** Trait hierarchies and intraspecific variability drive competitive interactions in Mediterranean annual plants. *Journal of Ecology* **107**: 2078–2089.
- Carmona CP, Bueno CG, Toussaint A, Träger S, Díaz S, Moora M, Munson AD, Pärtel M, Zobel M, Tamme R. 2021.** Fine-root traits in the global spectrum of plant form and function. *Nature* **597**: 683–687.
- Chapin FS. 1980.** The Mineral Nutrition of Wild Plants. *Annual Review of Ecology and Systematics* **11**: 233–260.
- Chen YH, Shapiro LR, Benrey B, Cibrián-Jaramillo A. 2017.** Back to the Origin: In Situ Studies Are Needed to Understand Selection during Crop Diversification. *Frontiers in Ecology and Evolution* **5**: 125.
- Cianciaruso MV, Batalha MA, Gaston KJ, Petchey OL. 2009.** Including intraspecific variability in functional diversity. *Ecology* **90**: 81–89.
- Colombo M, Montazeaud G, Viader V, Ecartot M, Prosperi J-M, David J, Fort F, Violle C, Fréville H. 2022.** A genome-wide analysis suggests pleiotropic effects of Green Revolution genes on shade avoidance in wheat. *Evolutionary Applications* **15**: 1594–1604.
- Craine JM. 2009.** Resource Strategies of Wild Plants. In: Resource Strategies of Wild Plants. Princeton University Press.
- Crick J c., Grime J p. 1987.** Morphological Plasticity and Mineral Nutrient Capture in Two Herbaceous Species of Contrasted Ecology. *New Phytologist* **107**: 403–414.
- Cunniff J, Wilkinson S, Charles M, Jones G, Rees M, Osborne CP. 2014.** Functional Traits Differ between Cereal Crop Progenitors and Other Wild Grasses Gathered in the Neolithic Fertile Crescent. *PLOS ONE* **9**: e87586.
- Darwin C. 1868.** *The Variation of Animals and Plants Under Domestication*. J. Murray.
- David J, Holtz Y, Ranwez V, Santoni S, Sarah G, Ardisson M, Poux G, Choulet F, Genthon C, Roumet P, et al. 2014.** Genotyping by sequencing transcriptomes in an evolutionary pre-breeding durum wheat population. *Molecular Breeding* **34**: 1531–1548.

- Day PR. 1973.** Genetic Variability of Crops. *Annual Review of Phytopathology* **11**: 293–312.
- De Kroon H, Mommer L, Nishiwaki A. 2003.** Root Competition: Towards a Mechanistic Understanding. In: De Kroon H, Visser EJW, eds. *Ecological Studies. Root Ecology*. Berlin, Heidelberg: Springer Berlin Heidelberg, 215–234.
- Dempewolf H, Baute G, Anderson J, Kilian B, Smith C, Guarino L. 2017.** Past and Future Use of Wild Relatives in Crop Breeding. *Crop Science* **57**: 1070–1082.
- Deng J, Ran J, Wang Z, Fan Z, Wang G, Ji M, Liu J, Wang Y, Liu J, Brown JH. 2012a.** Models and tests of optimal density and maximal yield for crop plants. *Proceedings of the National Academy of Sciences* **109**: 15823–15828.
- Deng J, Zuo W, Wang Z, Fan Z, Ji M, Wang G, Ran J, Zhao C, Liu J, Niklas KJ, et al. 2012b.** Insights into plant size-density relationships from models and agricultural crops. *Proceedings of the National Academy of Sciences* **109**: 8600–8605.
- Denison RF. 2015.** Evolutionary tradeoffs as opportunities to improve yield potential. *Field Crops Research* **182**: 3–8.
- Denison RF, Kiers ET, West SA. 2003.** Darwinian Agriculture: When Can Humans Find Solutions Beyond the Reach of Natural Selection? *The Quarterly Review of Biology* **78**: 145–168.
- Des Marais DL, Hernandez KM, Juenger TE. 2013.** Genotype-by-Environment Interaction and Plasticity: Exploring Genomic Responses of Plants to the Abiotic Environment. *Annual Review of Ecology, Evolution, and Systematics* **44**: 5–29.
- Diamond J. 2002.** Evolution, consequences and future of plant and animal domestication. *Nature* **418**: 700–707.
- Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Colin Prentice I, et al. 2016.** The global spectrum of plant form and function. *Nature* **529**: 167–171.
- Donald CM. 1968.** The breeding of crop ideotypes. *Euphytica* **17**: 385–403.
- Duarte CM, Sand-Jensen K, Nielsen SL, Enríquez S, Agustí S. 1995.** Comparative functional plant ecology: rationale and potentials. *Trends in Ecology & Evolution* **10**: 418–421.
- Duvick DN. 1986.** Plant breeding: Past achievements and expectations for the future. *Economic Botany* **40**: 289–297.
- Enquist BJ, West GB, Charnov EL, Brown JH. 1999.** Allometric scaling of production and life-history variation in vascular plants. *Nature* **401**: 907–911.
- Evenson RE, Gollin D. 2003.** Assessing the Impact of the Green Revolution, 1960 to 2000. *Science* **300**: 758–762.
- Fajardo A, Siefert A. 2018.** Intraspecific trait variation and the leaf economics spectrum across resource gradients and levels of organization. *Ecology* **99**: 1024–1030.
- Fischer RAT, Edmeades GO. 2010.** Breeding and Cereal Yield Progress. *Crop Science* **50**: S-85-S-98.

- Fox JW, Vasseur DA. 2008.** Character Convergence under Competition for Nutritionally Essential Resources. *The American Naturalist* **172**: 667–680.
- Freckleton RP, Watkinson AR. 2001.** Asymmetric competition between plant species. *Functional Ecology* **15**: 615–623.
- Freschet GT, Cornelissen JHC, Logtestijn RSPV, Aerts R. 2010.** Evidence of the ‘plant economics spectrum’ in a subarctic flora. *Journal of Ecology* **98**: 362–373.
- Freschet GT, Pagès L, Iversen CM, Comas LH, Rewald B, Roumet C, Klimešová J, Zadworny M, Poorter H, Postma JA, et al. 2021.** A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. *New Phytologist* **232**: 973–1122.
- Fuller DQ. 2007.** Contrasting Patterns in Crop Domestication and Domestication Rates: Recent Archaeobotanical Insights from the Old World. *Annals of Botany* **100**: 903–924.
- Fuller DQ, Allaby RG, Stevens C. 2010.** Domestication as innovation: the entanglement of techniques, technology and chance in the domestication of cereal crops. *World Archaeology* **42**: 13–28.
- Fuller DQ, Denham T, Arroyo-Kalin M, Lucas L, Stevens CJ, Qin L, Allaby RG, Purugganan MD. 2014.** Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record. *Proceedings of the National Academy of Sciences* **111**: 6147–6152.
- Gagliardi S, Martin AR, Filho E de MV, Rapidel B, Isaac ME. 2015.** Intraspecific leaf economic trait variation partially explains coffee performance across agroforestry management regimes. *Agriculture, Ecosystems & Environment* **200**: 151–160.
- Gallais A. 1984.** Use of indirect selection in plant breeding. In: 10th Eucarpia Congress: Efficiency in Plant Breeding. Wageningen, the Netherlands. 45–60.
- Gallais A. 2018.** Histoire de la génétique et de l’amélioration des plantes. *Histoire de la génétique et de l’amélioration des plantes*, 1–288.
- Garland T, Downs CJ, Ives AR. 2022.** Trade-Offs (and Constraints) in Organismal Biology. *Physiological and Biochemical Zoology* **95**: 82–112.
- Garnier E, Navas M-L, Grigulis K. 2016.** *Plant Functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties*. Oxford, UK: Oxford University Press.
- Gaudet CL, Keddy PA. 1988.** A comparative approach to predicting competitive ability from plant traits. *Nature* **334**: 242–243.
- Gepts P. 2004.** Crop Domestication as a Long-Term Selection Experiment. In: Janick J, ed. *Plant Breeding Reviews*. Oxford, UK: John Wiley & Sons, Inc., 1–44.
- Gepts P. 2006.** Plant Genetic Resources Conservation and Utilization: The Accomplishments and Future of a Societal Insurance Policy. *Crop Science* **46**: 2278–2292.
- Glazier DS. 2022.** Variable metabolic scaling breaks the law: from ‘Newtonian’ to ‘Darwinian’ approaches. *Proceedings of the Royal Society B: Biological Sciences* **289**: 20221605.

- Glémin S, Bataillon T. 2009.** A comparative view of the evolution of grasses under domestication. *New Phytologist* **183**: 273–290.
- Gold MV. 1999.** *Sustainable Agriculture: Definitions and Terms*. National Agricultural Library.
- Goldberg D. 1990.** Components of resource competition in plant communities. In: Perspectives on plant competition. 27–49.
- Goldberg DE. 1997.** Competitive ability: definitions, contingency and correlated traits. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **351**: 1377–1385.
- Goldberg DE, Fleetwood L. 1987.** Competitive Effect and Response in Four Annual Plants. *The Journal of Ecology* **75**: 1131.
- Goldberg DE, Landa K. 1991.** Competitive Effect and Response: Hierarchies and Correlated Traits in the Early Stages of Competition. *Journal of Ecology* **79**: 1013–1030.
- Gómez-Fernández A. 2023.** Plant size variation in crops: causes, mechanisms and consequences.
- Gould SJ. 1966.** Allometry and Size in Ontogeny and Phylogeny. *Biological Reviews* **41**: 587–638.
- Grace J. 2012.** *Perspectives on Plant Competition*. Elsevier.
- Grime JP. 1977.** Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist* **111**: 1169–1194.
- Grime JP. 1979.** Primary strategies in plants: Transactions of the Botanical Society of Edinburgh: Vol 43, No 2.
- Gross N, Le Bagousse-Pinguet Y, Liancourt P, Berdugo M, Gotelli NJ, Maestre FT. 2017.** Functional trait diversity maximizes ecosystem multifunctionality. *Nature ecology & evolution* **1**: 0132.
- Grossman JD, Rice KJ. 2012.** Evolution of root plasticity responses to variation in soil nutrient distribution and concentration. *Evolutionary Applications* **5**: 850–857.
- Hardin G. 1968.** The Tragedy of the Commons. *Science* **162**: 1243–1248.
- Harlan JR, Gepts P, Famula TR, Bettinger RL, Brush SB, Damania AB, McGuire PE, Qualset CO. 2012.** *Biodiversity in Agriculture: Domestication, Evolution, and Sustainability*. Cambridge University Press.
- Harlan JR, de Wet JMJ, Price EG. 1973.** Comparative Evolution of Cereals. *Evolution* **27**: 311–325.
- Hawkes JG. 2013.** *The Diversity of Crop Plants*. Harvard University Press.
- Hay RKM. 1995.** Harvest index: a review of its use in plant breeding and crop physiology. *Annals of Applied Biology* **126**: 197–216.
- Hermes DA, Mattson WJ. 1992.** The Dilemma of Plants: To Grow or Defend. *The Quarterly Review of Biology* **67**: 283–335.

- Hu Y-K, Pan X, Liu G-F, Li W-B, Dai W-H, Tang S-L, Zhang Y-L, Xiao T, Chen L-Y, Xiong W, et al. 2015.** Novel evidence for within-species leaf economics spectrum at multiple spatial scales. *Frontiers in Plant Science* **6**: 901.
- Hufford MB, Berny Mier Y Teran JC, Gepts P. 2019.** Crop Biodiversity: An Unfinished Magnum Opus of Nature. *Annual Review of Plant Biology* **70**: 727–751.
- Huxley JS. 1924.** Constant Differential Growth-Ratios and their Significance. *Nature* **114**: 895–896.
- Jennings PR, De Jesus J. 1968.** Studies on competition in rice I. Competition in mixtures of varieties. *Evolution* **22**: 119–124.
- Jones G. 2005.** Garden cultivation of staple crops and its implications for settlement location and continuity. *World Archaeology* **37**: 164–176.
- Jones G, Kluyver T, Preece C, Swarbrick J, Forster E, Wallace M, Charles M, Rees M, Osborne CP. 2021.** The origins of agriculture: Intentions and consequences. *Journal of Archaeological Science* **125**: 105290.
- Jung V, Violle C, Mondy C, Hoffmann L, Muller S. 2010.** Intraspecific variability and trait-based community assembly. *Journal of Ecology* **98**: 1134–1140.
- Kebrom TH, Brutnell TP. 2007.** The molecular analysis of the shade avoidance syndrome in the grasses has begun. *Journal of Experimental Botany* **58**: 3079–3089.
- Keddy PA. 1992.** A Pragmatic Approach to Functional Ecology. *Functional Ecology* **6**: 621.
- Keddy PA, Shipley B. 1989.** Competitive Hierarchies in Herbaceous Plant Communities. *Oikos* **54**: 234–241.
- Khalifa MA, Qualset CO. 1974.** Intergenotypic Competition Between Tall and Dwarf Wheats. I. In Mechanical Mixtures I. *Crop Science* **14**: 795–799.
- Khush GS. 2001.** Green revolution: the way forward. *Nature Reviews Genetics* **2**: 815–822.
- Kleiber M. 1947.** Body size and metabolic rate. *Physiological Reviews* **27**: 511–541.
- Kozak M, Mađry W. 2006.** Note on yield component analysis. *Cereal Research Communications* **34**: 933–940.
- Kramer-Walter KR, Bellingham PJ, Millar TR, Smissen RD, Richardson SJ, Laughlin DC. 2016.** Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology* **104**: 1299–1310.
- Laforest-Lapointe I, Martínez-Vilalta J, Retana J. 2014.** Intraspecific variability in functional traits matters: case study of Scots pine. *Oecologia* **175**: 1337–1348.
- Larson G, Piperno DR, Allaby RG, Purugganan MD, Andersson L, Arroyo-Kalin M, Barton L, Climer Vigueira C, Denham T, Dobney K, et al. 2014.** Current perspectives and the future of domestication studies. *Proceedings of the National Academy of Sciences* **111**: 6139–6146.

- Lavorel S, Garnier E. 2002.** Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**: 545–556.
- Lee G-A, Crawford GW, Liu L, Chen X. 2007.** Plants and people from the Early Neolithic to Shang periods in North China. *Proceedings of the National Academy of Sciences* **104**: 1087–1092.
- Lesk C, Rowhani P, Ramankutty N. 2016.** Influence of extreme weather disasters on global crop production. *Nature* **529**: 84–87.
- Liu Y-X, Zhang W-P, Sun J-H, Li X-F, Christie P, Li L. 2015.** High morphological and physiological plasticity of wheat roots is conducive to higher competitive ability of wheat than maize in intercropping systems. *Plant and Soil* **397**: 387–399.
- MacLaren C, Waswa W, Aliyu KT, Claessens L, Mead A, Schöb C, Vanlauwe B, Storkey J. 2023.** Predicting intercrop competition, facilitation, and productivity from simple functional traits. *Field Crops Research* **297**: 108926.
- Mansfield BD, Mumm RH. 2014.** Survey of Plant Density Tolerance in U.S. Maize Germplasm. *Crop Science* **54**: 157–173.
- Martin AR, Isaac ME. 2015.** REVIEW: Plant functional traits in agroecosystems: a blueprint for research. *Journal of Applied Ecology* **52**: 1425–1435.
- Martín-Robles N, Morente-López J, Freschet GT, Poorter H, Roumet C, Milla R. 2019.** Root traits of herbaceous crops: Pre-adaptation to cultivation or evolution under domestication? *Functional Ecology* **33**: 273–285.
- Matesanz S, Milla R. 2018.** Differential plasticity to water and nutrients between crops and their wild progenitors. *Environmental and Experimental Botany* **145**: 54–63.
- McKey DB, Elias M, Pujol B, Duputié A. 2012.** Ecological Approaches to Crop Domestication. In: Gepts P, Famula TR, Bettinger RL, Brush SB, Damania AB, McGuire PE, Qualset CO, eds. *Biodiversity in Agriculture*. Cambridge University Press, 377–406.
- Mercuri AM, Fornaciari R, Gallinaro M, Vanin S, di Lernia S. 2018.** Plant behaviour from human imprints and the cultivation of wild cereals in Holocene Sahara. *Nature Plants* **4**: 71–81.
- Meyer RS, DuVal AE, Jensen HR. 2012.** Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops. *New Phytologist* **196**: 29–48.
- Meyer RS, Purugganan MD. 2013.** Evolution of crop species: genetics of domestication and diversification. *Nature Reviews Genetics* **14**: 840–852.
- Milla R. 2023.** Phenotypic evolution of agricultural crops. *Functional Ecology* **37**: 976–988.
- Milla R, Bastida JM, Turcotte MM, Jones G, Violle C, Osborne CP, Chacón-Labela J, Sosinski ÊE, Kattge J, Laughlin DC, et al. 2018.** Phylogenetic patterns and phenotypic profiles of the species of plants and mammals farmed for food. *Nature Ecology & Evolution* **2**: 1808–1817.
- Milla R, Matesanz S. 2017.** Growing larger with domestication: a matter of physiology, morphology or allocation? *Plant Biology* **19**: 475–483.

- Milla R, Morente-López J, Alonso-Rodrigo JM, Martín-Robles N, Stuart Chapin F. 2014.** Shifts and disruptions in resource-use trait syndromes during the evolution of herbaceous crops. *Proceedings of the Royal Society B: Biological Sciences* **281**: 20141429.
- Milla, Osborne CP, Turcotte MM, Violle C. 2015.** Plant domestication through an ecological lens. *Trends in Ecology & Evolution* **30**: 463–469.
- Mirnezhad M, Romero-González RR, Leiss KA, Choi YH, Verpoorte R, Klinkhamer PGL. 2010.** Metabolomic analysis of host plant resistance to thrips in wild and cultivated tomatoes. *Phytochemical Analysis* **21**: 110–117.
- Montazeaud G. 2019.** Diversité vs uniformité : Combiner les approches écologiques et évolutives pour concevoir des systèmes de culture durables.
- Montazeaud G, Violle C, Roumet P, Rocher A, Ecartot M, Compan F, Maillet G, Fort F, Fréville H. 2020.** Multifaceted functional diversity for multifaceted crop yield: Towards ecological assembly rules for varietal mixtures. *Journal of Applied Ecology* **57**: 2285–2295.
- Niinemets Ü. 2015.** Is there a species spectrum within the world-wide leaf economics spectrum? Major variations in leaf functional traits in the Mediterranean sclerophyll *Quercus ilex*. *New Phytologist* **205**: 79–96.
- Niklas KJ. 2004.** Plant allometry: is there a grand unifying theory? *Biological Reviews* **79**: 871–889.
- Niklas KJ, Marler TE. 2007.** *Carica papaya* (Caricaceae): a case study into the effects of domestication on plant vegetative growth and reproduction. *American Journal of Botany* **94**: 999–1002.
- Niu Y, Chen T, Zhao C, Zhou M. 2022.** Lodging prevention in cereals: Morphological, biochemical, anatomical traits and their molecular mechanisms, management and breeding strategies. *Field Crops Research* **289**: 108733.
- Novoplansky A. 2009.** Picking battles wisely: plant behaviour under competition. *Plant, Cell & Environment* **32**: 726–741.
- Orr HA. 2009.** Fitness and its role in evolutionary genetics. *Nature Reviews Genetics* **10**: 531–539.
- Phillips PC, Arnold SJ. 1989.** Visualizing Multivariate Selection. *Evolution* **43**: 1209–1222.
- Poorter H, Jagodzinski AM, Ruiz-Peinado R, Kuyah S, Luo Y, Oleksyn J, Usoltsev VA, Buckley TN, Reich PB, Sack L. 2015.** How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytologist* **208**: 736–749.
- Poorter H, Lambers H. 1986.** Growth and competitive ability of a highly plastic and a marginally plastic genotype of *Plantago major* in a fluctuating environment. *Physiologia Plantarum* **67**: 217–222.
- Poorter H, Ryser P. 2015.** The limits to leaf and root plasticity: what is so special about specific root length? *New Phytologist* **206**: 1188–1190.
- Postma JA, Kuppe C, Owen MR, Mellor N, Griffiths M, Bennett MJ, Lynch JP, Watt M. 2017.** OpenSimRoot: widening the scope and application of root architectural models. *The New Phytologist* **215**: 1274–1286.

Preece C, Clamp NF, Warham G, Charles M, Rees M, Jones G, Osborne CP. 2018. Cereal progenitors differ in stand harvest characteristics from related wild grasses. *Journal of Ecology* **106**: 1286–1297.

Preece C, Livarda A, Wallace M, Martin G, Charles M, Christin P-A, Jones G, Rees M, Osborne CP. 2015. Were Fertile Crescent crop progenitors higher yielding than other wild species that were never domesticated? *New Phytologist* **207**: 905–913.

Purugganan MD. 2022. What is domestication? *Trends in Ecology & Evolution* **37**: 663–671.

Purugganan MD, Fuller DQ. 2009. The nature of selection during plant domestication. *Nature* **457**: 843–848.

Reich PB. 2014. The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**: 275–301.

Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences* **94**: 13730–13734.

Reif JC, Zhang P, Dreisigacker S, Warburton ML, van Ginkel M, Hoisington D, Bohn M, Melchinger AE. 2005. Wheat genetic diversity trends during domestication and breeding. *Theoretical and Applied Genetics* **110**: 859–864.

Reynolds M, Foulkes J, Furbank R, Griffiths S, King J, Murchie E, Parry M, Slafer G. 2012. Achieving yield gains in wheat. *Plant, Cell & Environment* **35**: 1799–1823.

Rimbert H, Darrier B, Navarro J, Kitt J, Choulet F, Leveugle M, Duarte J, Rivière N, Eversole K, Consortium on behalf of TIWGS, et al. 2018. High throughput SNP discovery and genotyping in hexaploid wheat. *PLOS ONE* **13**: e0186329.

Rindos D, Aschmann H, Bellwood P, Ceci L, Cohen MN, Hutchinson J, Santley RS, Shaffer JG, Shaw T. 1980. Symbiosis, Instability, and the Origins and Spread of Agriculture: A New Model [and Comments and Reply]. *Current Anthropology* **21**: 751–772.

Riva EG de la, Tosto A, Pérez-Ramos IM, Navarro-Fernández CM, Olmo M, Anten NPR, Marañón T, Villar R. 2016. A plant economics spectrum in Mediterranean forests along environmental gradients: is there coordination among leaf, stem and root traits? *Journal of Vegetation Science* **27**: 187–199.

Rodriguez-Saona C, Vorsa N, Singh AP, Johnson-Cicalese J, Szendrei Z, Mescher MC, Frost CJ. 2011. Tracing the history of plant traits under domestication in cranberries: potential consequences on anti-herbivore defences. *Journal of Experimental Botany* **62**: 2633–2644.

Rolhauser AG, Windfeld E, Hanson S, Wittman H, Thoreau C, Lyon A, Isaac ME. 2022. A trait–environment relationship approach to participatory plant breeding for organic agriculture. *The New Phytologist* **235**: 1018–1031.

Roucou A, Violle C, Fort F, Roumet P, Ecartot M, Vile D. 2018. Shifts in plant functional strategies over the course of wheat domestication. *Journal of Applied Ecology* **55**: 25–37.

Saqalli M, Salavert A, Bréhard S, Bendrey R, Vigne J-D, Tresset A. 2014. Revisiting and modelling the woodland farming system of the early Neolithic Linear Pottery Culture (LBK), 5600–4900 b.c. *Vegetation History and Archaeobotany* **23**: 37–50.

- Sartori K, Vasseur F, Violle C, Baron E, Gerard M, Rowe N, Ayala-Garay O, Christophe A, Jalón LG de, Masclef D, et al. 2019.** Leaf economics and slow-fast adaptation across the geographic range of *Arabidopsis thaliana*. *Scientific Reports* **9**: 10758.
- Schlichting CD. 1989.** Phenotypic Integration and Environmental Change: What are the consequences of differential phenotypic plasticity of traits? *BioScience* **39**: 460–464.
- Schmid B. 1992.** Phenotypic variation in plants. *Evolutionary trends in plants*.
- Schmidt-Nielsen K. 1984.** *Scaling: Why is Animal Size So Important?* Cambridge University Press.
- Shoval O, Sheftel H, Shinar G, Hart Y, Ramote O, Mayo A, Dekel E, Kavanagh K, Alon U. 2012.** Evolutionary Trade-Offs, Pareto Optimality, and the Geometry of Phenotype Space. *Science* **336**: 1157–1160.
- Singh RB. 2000.** Environmental consequences of agricultural development: a case study from the Green Revolution state of Haryana, India. *Agriculture, Ecosystems & Environment* **82**: 97–103.
- Smith H, Whitelam GC. 1997.** The shade avoidance syndrome: multiple responses mediated by multiple phytochromes. *Plant, Cell & Environment* **20**: 840–844.
- Sorrensen-Cothorn KA, Ford ED, Sprugel DG. 1993.** A Model of Competition Incorporating Plasticity through Modular Foliage and Crown Development. *Ecological Monographs* **63**: 277–304.
- Sultan SE. 2000.** Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science* **5**: 537–542.
- Tanno K, Willcox G. 2012.** Distinguishing wild and domestic wheat and barley spikelets from early Holocene sites in the Near East. *Vegetation History and Archaeobotany* **21**: 107–115.
- Taylor G, Thomas A. 2014.** *Evolutionary Biomechanics: Selection, Phylogeny, and Constraint*. OUP Oxford.
- Tedone L, Ali SA, Mastro GD, Tedone L, Ali SA, Mastro GD. 2017.** Optimization of Nitrogen in Durum Wheat in the Mediterranean Climate: The Agronomical Aspect and Greenhouse Gas (GHG) Emissions. In: Nitrogen in Agriculture - Updates. IntechOpen.
- Thompson K, Grime JP. 1988.** Competition Reconsidered-A Reply to Tilman. *British Ecological Society* **2**: 114–116.
- Tian Z, Wang J-W, Li J, Han B. 2021.** Designing future crops: challenges and strategies for sustainable agriculture. *The Plant Journal* **105**: 1165–1178.
- Tilman D. 1982.** *Resource Competition and Community Structure*. Princeton University Press.
- Tilman D. 1987.** On the Meaning of Competition and the Mechanisms of Competitive Superiority. *Functional Ecology* **1**: 304–315.
- Tilman D. 1998.** The greening of the green revolution. *Nature* **396**: 211–212.

- Tilman D. 1999.** Global environmental impacts of agricultural expansion: The need for sustainable and efficient practices. *Proceedings of the National Academy of Sciences* **96**: 5995–6000.
- Tilman D. 2001.** Functional diversity. *Encyclopedia of biodiversity* **3**: 109–120.
- Tilman D, Fargione J, Wolff B, D’Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D. 2001.** Forecasting Agriculturally Driven Global Environmental Change. *Science* **292**: 281–284.
- de Tombeur F, Lemoine T, Violle C, Fréville H, Thorne SJ, Hartley SE, Lambers H, Fort F. 2022.** Nitrogen availability and plant–plant interactions drive leaf silicon concentration in wheat genotypes. *Functional Ecology* **36**: 1–12.
- Turcotte MM, Levine JM. 2016.** Phenotypic Plasticity and Species Coexistence. *Trends in Ecology & Evolution* **31**: 803–813.
- Tzarfati R, Saranga Y, Barak V, Gopher A, Korol AB, Abbo S. 2013.** Threshing efficiency as an incentive for rapid domestication of emmer wheat. *Annals of Botany* **112**: 829–837.
- Vargas-Ponce O, Zizumbo-Villarreal D, Martínez-Castillo J, Coello-Coello J, Colunga-GarcíaMarín P. 2009.** Diversity and structure of landraces of Agave grown for spirits under traditional agriculture: A comparison with wild populations of *A. angustifolia* (Agavaceae) and commercial plantations of *A. tequilana*. *American Journal of Botany* **96**: 448–457.
- Vasseur F, Exposito-Alonso M, Ayala-Garay OJ, Wang G, Enquist BJ, Vile D, Violle C, Weigel D. 2018.** Adaptive diversification of growth allometry in the plant *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences* **115**: 3416–3421.
- Vasseur F, Violle C, Enquist BJ, Granier C, Vile D. 2012.** A common genetic basis to the origin of the leaf economics spectrum and metabolic scaling allometry. *Ecology Letters* **15**: 1149–1157.
- Vermeulen PJ, Anten NPR, Schieving F, Werger MJA, During HJ. 2008.** Height convergence in response to neighbour growth: genotypic differences in the stoloniferous plant *Potentilla reptans*. *New Phytologist* **177**: 688–697.
- Villalobos FJ, Sadras VO, Fereres E. 2016.** Plant Density and Competition. In: Villalobos FJ, Fereres E, eds. *Principles of Agronomy for Sustainable Agriculture*. Cham: Springer International Publishing, 159–168.
- Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier J. 2012.** The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* **27**: 244–252.
- Violle C, Garnier E, Lecoœur J, Roumet C, Podgeur C, Blanchard A, Navas M-L. 2009.** Competition, traits and resource depletion in plant communities. *Oecologia* **160**: 747–755.
- Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007.** Let the concept of trait be functional! *Oikos* **116**: 882–892.

- Weigelt A, Mommer L, Andraczek K, Iversen CM, Bergmann J, Bruelheide H, Fan Y, Freschet GT, Guerrero-Ramírez NR, Kattge J, et al. 2021.** An integrated framework of plant form and function: the belowground perspective. *New Phytologist* **232**: 42–59.
- Weiner J. 1990.** Asymmetric competition in plant populations. *Trends in Ecology & Evolution* **5**: 360–364.
- Weiner J. 2003.** Ecology – the science of agriculture in the 21st century. *The Journal of Agricultural Science* **141**: 371–377.
- Weiner J, Andersen SB, Wille WK-M, Griepentrog HW, Olsen JM. 2010.** Evolutionary Agroecology: the potential for cooperative, high density, weed-suppressing cereals. *Evolutionary Applications* **3**: 473–479.
- Weiner J, Campbell LG, Pino J, Echarte L. 2009.** The allometry of reproduction within plant populations. *Journal of Ecology* **97**: 1220–1233.
- Weiner J, Freckleton RP. 2010.** Constant Final Yield. *Annual Review of Ecology, Evolution, and Systematics* **41**: 173–192.
- Weiss E, Kislev ME, Hartmann A. 2006.** Autonomous Cultivation Before Domestication. *Science* **312**: 1608–1610.
- West GB, Brown JH. 2005.** The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization. *Journal of Experimental Biology* **208**: 1575–1592.
- West GB, Brown JH, Enquist BJ. 1997.** A General Model for the Origin of Allometric Scaling Laws in Biology. *Science* **276**: 122–126.
- West GB, Brown JH, Enquist BJ. 1999.** A general model for the structure and allometry of plant vascular systems. *Nature* **400**: 664–667.
- Westoby M. 1984.** The Self-Thinning Rule. In: MacFadyen A, Ford ED, eds. *Advances in Ecological Research*. Academic Press, 167–225.
- Westoby M. 1998.** A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**: 213–227.
- Wezel A, Bellon S, Doré T, Francis C, Vallod D, David C. 2009.** Agroecology as a science, a movement and a practice. A review. *Agronomy for Sustainable Development* **29**: 503–515.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, et al. 2004.** The worldwide leaf economics spectrum. *Nature* **428**: 821–827.
- Wright JP, Sutton-Grier A. 2012.** Does the leaf economic spectrum hold within local species pools across varying environmental conditions? *Functional Ecology* **26**: 1390–1398.
- Xiao S, Chen S-Y, Zhao L-Q, Wang G. 2006.** Density Effects on Plant Height Growth and Inequality in Sunflower Populations. *Journal of Integrative Plant Biology* **48**: 513–519.
- Xynias IN, Mylonas I, Korpetis EG, Ninou E, Tsaballa A, Avdikos ID, Mavromatis AG. 2020.** Durum Wheat Breeding in the Mediterranean Region: Current Status and Future Prospects. *Agronomy* **10**: 432.

Zeven AC. 1973. Dr Th. H. Engelbrecht's views on the origin of cultivated plants. *Euphytica* **22**: 279–286.

Zeven AC. 1998. Landraces: A review of definitions and classifications. *Euphytica*: 127–139.

Zeven AC, Wet JMJ de. 1982. *Dictionary of cultivated plants and their regions of diversity: excluding most ornamentals, forest trees and lower plants.* Wageningen: PUDOC.

Zhang H, Mittal N, Leamy LJ, Barazani O, Song B-H. 2017. Back into the wild—Apply untapped genetic diversity of wild relatives for crop improvement. *Evolutionary Applications* **10**: 5–24.

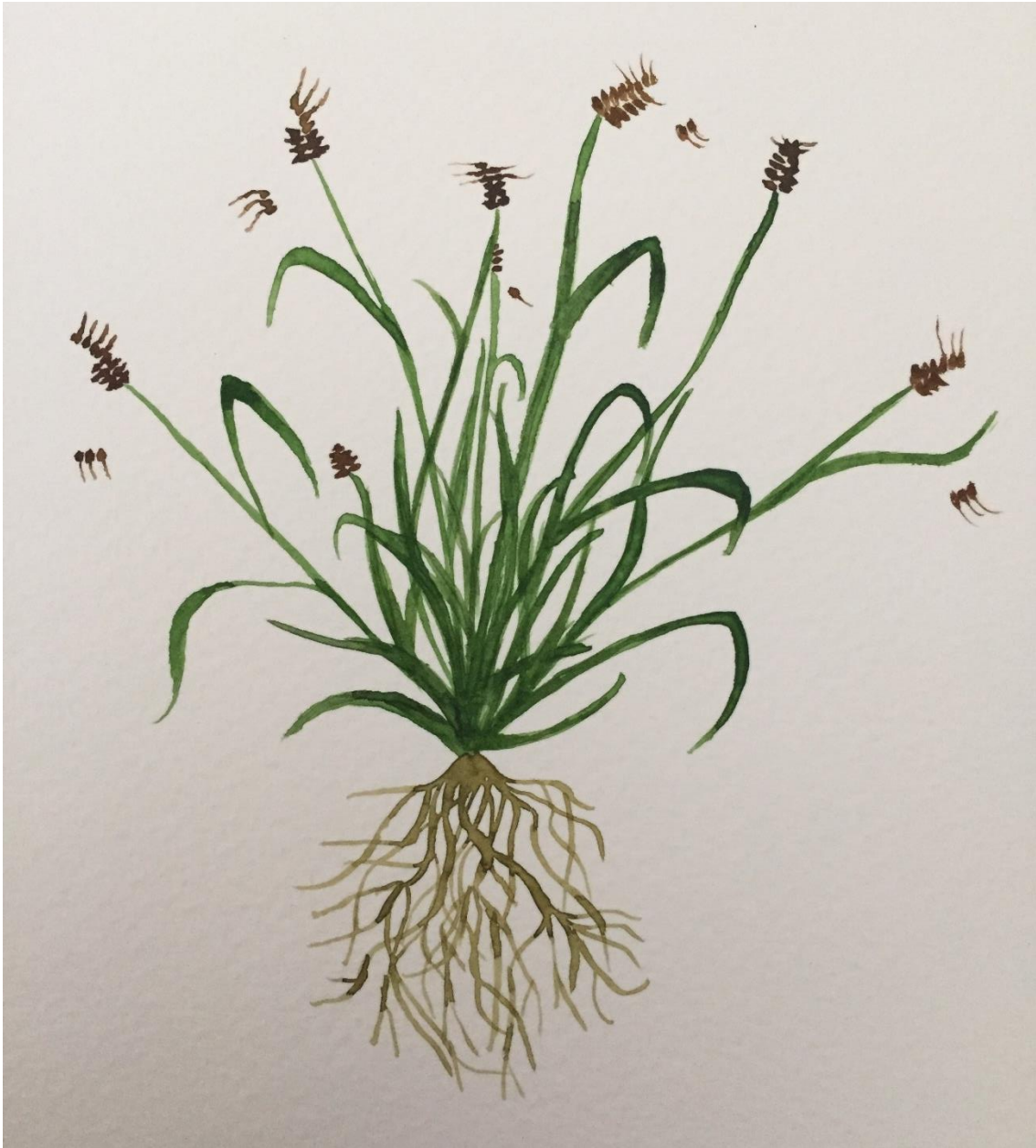
Zhang D-Y, Sun G-J, Jiang X-H. 1999. Donald's ideotype and growth redundancy: a game theoretical analysis. *Field Crops Research* **61**: 179–187.

Zhu J, van der Werf W, Anten NPR, Vos J, Evers JB. 2015. The contribution of phenotypic plasticity to complementary light capture in plant mixtures. *New Phytologist* **207**: 1213–1222.

Zhu J, van der Werf W, Vos J, Anten N. P. R., van der Putten P. E. L., Evers J B. 2016. High productivity of wheat intercropped with maize is associated with plant architectural responses. *Annals of Applied Biology* **168**: 357–372.

Zohary D. 2004. Unconscious selection and the evolution of domesticated Plants. *Economic Botany* **58**: 5–10.

Zohary D, Hopf M. 2000. Domestication of plants in the Old World: the origin and spread of cultivated plants in West Asia, Europe and the Nile Valley. *Domestication of plants in the Old World: the origin and spread of cultivated plants in West Asia, Europe and the Nile Valley.* Oxford university press.



Ancêtre sauvage de blé dur

A. Rimlinger

CHAPITRE 1

Plant trait relationships are maintained within a major crop species: lack of artificial selection signal and potential for improved agronomic performance

Article publié

Lemoine, T., Violle, C., Montazeaud, G., Isaac, M. E., Rocher, A., Fréville, H., & Fort, F. (2023). Plant trait relationships are maintained within a major crop species: lack of artificial selection signal and potential for improved agronomic performance. *New Phytologist*.

I. Présentation générale

Les pressions de sélection associées à la domestication et à la sélection moderne ont conduit à de multiples changements génétiques et phénotypiques chez les plantes cultivées. Les corrélations entre les traits ont alors pu être fragilisées ou modifiées (Roucou *et al.*, 2018; Cantarel *et al.*, 2020). Certaines corrélations entre traits ont également pu apparaître ou au contraire disparaître du fait de la sélection indirecte (Milla *et al.*, 2014, 2015). Les compromis représentent cependant des contraintes écophysiologiques fortes sur la variation phénotypique des plantes (Reich, 2014; Díaz *et al.*, 2016; Weigelt *et al.*, 2021). Peuvent-ils donc être modulés au sein d'une espèce et d'une espèce cultivée ? **L'objectif de cette première partie est de tester si les compromis fonctionnels observés au niveau interspécifique se maintiennent au sein d'une espèce cultivée.** Nous nous attendons à des différences dans l'espace fonctionnel du blé dur par rapport à l'espace interspécifique (Weigelt *et al.*, 2021) du fait de l'adaptation du blé aux environnements cultivés et de la sélection artificielle.

Pour le tester, nous construisons deux espaces phénotypiques, un espace fonctionnel et un espace agronomique. Ces espaces sont construits à partir des traits fonctionnels aériens et souterrains et des traits agronomiques mesurés au champ sur 179 lignées consanguines de blé dur, provenant de la population de pré-sélection EPO développée par l'INRAE de Montpellier. EPO est une population composite génétiquement diversifiée, fondée à partir de sous-espèces de blé, sauvage, primitive et moderne (David *et al.*, 2014). Elle est donc caractérisée par différents degrés de sélection artificielle. Nous testons par ailleurs si et comment la sélection artificielle a influencé la structure de l'espace des traits fonctionnels et agronomiques. Pour cela, nous estimons une distance génétique entre chaque génotype EPO et le compartiment élite du blé dur. Nous considérons que plus la distance génétique par rapport au compartiment élite est faible, plus la sélection artificielle est forte, le compartiment élite ayant été fortement sélectionné pendant la Révolution Verte. Dans cette étude, nous démontrons que les covariations de traits chez le blé dur étaient structurées par les mêmes compromis que ceux décrits au niveau interspécifique. Nous trouvons deux axes majeurs : un axe de stratégie d'exploration du sol et un axe illustrant le compromis de retour sur investissement « rapide-lent ». Nous détectons par ailleurs un effet de la distance génétique aux élites sur la variation des traits agronomiques, confirmant une forte empreinte de la sélection

artificielle sur les traits d'intérêts agronomiques. Les génotypes EPO qui partagent le plus de similitudes alléliques avec le compartiment élite ont un rendement en grain plus élevé. Cependant, dans cette étude nous ne détectons pas d'effet de la sélection artificielle sur le positionnement des génotypes dans l'espace phénotypique, suggérant que les compromis entre les traits fonctionnels sont difficiles à franchir.

Dans une seconde partie, nous analysons si certaines combinaisons de traits fonctionnels aériens et souterrains peuvent expliquer la variation de la performance agronomique du blé dur au champ. Les traits fonctionnels sont étroitement liés à la performance des plantes et indirectement à leur valeur sélective (Arnold, 1983; Violle *et al.*, 2007). La performance d'une plante reste cependant compliquée à prédire car elle est liée à une multitude de traits qui covarient les uns avec les autres (Violle *et al.*, 2007). Nous utilisons donc une approche statistique multivariée afin d'identifier les combinaisons de traits qui expliquent le mieux la performance agronomique des peuplements mono-génotypiques de blé dur. Dans ce chapitre, nous identifions des combinaisons de traits aériens et souterrains liées à la performance agronomique (rendement en grain, effort reproducteur, biomasse totale) de différents génotypes de blé dur. Ces résultats permettent de montrer que les traits impliqués dans la variation de la performance chez le blé sont portés par différents axes de variation impliquant l'entièreté du phénotype des plantes. Par ailleurs, notre étude montre également que différentes combinaisons de traits peuvent conduire à une même performance (Koehl, 1996; Wainwright *et al.*, 2005).

II. Keywords

Agronomic trait, crop domestication, durum wheat, phenotypic space, plant functional trait, trait-to-performance mapping

III. Abstract

- The exploration of phenotypic spaces of large sets of plant species has considerably increased our understanding of diversification processes in the plant kingdom. Nevertheless, such advances have predominantly relied on interspecific comparisons that hold several limitations.
- Here, we grew in the field a unique set of 179 inbred lines of durum wheat, *Triticum turgidum* spp. *durum*, characterized by variable degrees of artificial selection. We measured aboveground and belowground traits as well as agronomic traits to explore the functional and agronomic trait spaces, and to investigate trait-to-agronomic performance relationships.
- We showed that the wheat functional trait space shared commonalities with global cross-species spaces previously described, with two main axes of variation: a root foraging axis and a slow-fast trade-off axis. Moreover, we detected a clear signature of artificial selection on the variation of agronomic traits, unlike functional traits. Interestingly, we identified alternative phenotypic combinations that can optimize crop performance.
- Our work brings insightful knowledge about the structure of phenotypic spaces of domesticated plants and the maintenance of phenotypic trade-offs in response to artificial selection, with implications for trade-off-free and multi-criteria selection in plant breeding.

IV. Introduction

Characterizing the constraints shaping the diversification of life has long been debated in ecology and evolution (e.g., Gould *et al.*, 1997; Barton & Partridge, 2000; Grubb, 2016; Garland *et al.*, 2022). For a long time, ecology and evolution, micro- and macroevolution, diverged in the way

these constraints can be revealed. Over the last decades, plant comparative ecology has brought interesting insights by exploring the covariations between plant traits from a multivariate perspective (Garnier *et al.*, 2016). Indeed, studies comparing the relative positions of species in a multivariate trait space suggest that natural selection has shaped plant phenotypic diversity within an “envelope of constraints” (Ackerly *et al.*, 2000; Donovan *et al.*, 2011; Reich, 2014). Interspecific comparisons remain limited in their scope though, and the effects of selection cannot be deeply explored. Conversely, intraspecific comparisons are, by nature, better adapted to test the role of selection on phenotypic diversity, but their generalisation ability is low. Finding commonalities and peculiarities between intra- and interspecific phenotypic spaces appears as a promising avenue to test the robustness of ecological diversification laws.

Identifying independent dimensions of variation to document and understand phenotypic diversification across the plant kingdom is pivotal in plant functional ecology (Westoby *et al.*, 2002; Diaz *et al.*, 2004; Díaz *et al.*, 2016). These dimensions - axes of specialization - are traditionally approximated by a set of plant functional traits, defined as any morphological, phenological and physiological feature measurable at the individual scale and that impacts plant survival, growth and reproduction (Grime, 1977; Violle *et al.*, 2007; Garnier *et al.*, 2016). In interspecific comparisons, functional traits have been widely documented as proxies of organismal functions (e.g., light interception, soil nutrient acquisition and use) and of ecological strategies depicting plant adaptation to different environmental constraints (Grime, 1977; Westoby *et al.*, 2002; Diaz *et al.*, 2004) and resources’ use economy (Wright *et al.*, 2004; Garland *et al.*, 2022). Importantly, several traits need to be considered to accurately depict the whole phenotype (Laughlin, 2014; Mouillot *et al.*, 2021). A notable example is the study by Díaz *et al.* (2016) who summarized the phenotypic variation of vascular plants by a six-dimensional trait space. The authors identified two main axes of variation, one size-related axis, which discriminates small herbaceous plants that produce small diaspores from big trees with large diaspores, and another axis depicting a resource acquisition-conservation trade-off captured at the leaf level (the so-called leaf economics spectrum – LES –: Wright *et al.*, 2004). The recent incorporation of roots in these analyses has highlighted novel independent dimensions driven by root traits involved in soil resources’ economy (Weemstra *et al.*, 2016; Weigelt *et al.*, 2021), which strengthens the need to integrate the ‘hidden’ part of plants to grasp the multiple facets of resource foraging strategies (Bergmann & Weigelt, 2020). Overall, global trait-based analyses have been very fruitful in

revealing robust trait covariations that together shape and constrain cross-species functional spaces (Walker *et al.*, 2017). However, despite these efforts, the mechanisms driving plant functional spaces are still poorly known, partly because interspecific comparisons are inherently biased by phylogenetic signals (Garnier *et al.*, 2016). Even if recent evidence suggests commonalities when comparing intraspecific LES to interspecific LES (Vasseur *et al.*, 2012; Sartori *et al.*, 2019), the aboveground and belowground space of plant forms and functions still remain to be thoroughly assessed at the intraspecific level.

The fundamental constraints underlying functional trait spaces should delineate a fitness landscape in which certain combinations of traits lead to higher performances than others (Laughlin & Messier, 2015; Laughlin *et al.*, 2020). Even if the functional trait-to-performance linkage is a central tenet of trait-based ecology (Arnold, 1983; Violle *et al.*, 2007; Shipley *et al.*, 2016), interspecific analyses have reported weak and often contradictory findings regarding the functional drivers of plant performances (e.g., Adler *et al.*, 2014; Garnier *et al.*, 2018; Salguero-Gómez *et al.*, 2018; Yang, Cao and Swenson, 2018). A first reason is that such a linkage is probably species- and environment-dependent, and thus hardly detectable through interspecific comparisons (but see Rolhauser *et al.*, 2022). A second reason is that plant performance, and plant reproductive performance in particular, is multidimensional. This is well-known in crop science where agronomic performance is classically described by several agronomic traits such as grain yield, number of spikes per m², number of seeds per spike and thousand kernel weight (Bulman & Hunt, 1988; Kozak & Mađry, 2006), whose variation is constrained and structured within an agronomic trait space defined here as a multidimensional space reflecting major trade-offs among agronomic traits. A third reason is that the multidimensional nature of plant performance involves the interaction of several physiological and biomechanical properties of the organism, which can result in redundant mapping of plant performance and the existence of multiple peaks in the fitness landscape (Laughlin & Messier, 2015). In fact, it has long been recognized that numerous phenotypic combinations can yield to similar performance values (Koehl, 1996; Wainwright *et al.*, 2005). Such a ‘many-to-one’ mapping has already been discussed in the evolutionary biology literature (e.g., Wainwright *et al.*, 2005), but hardly in functional ecology (e.g., Marks & Lechowicz, 2006) despite its putative major role in shaping patterns of diversification in complex physiological systems (Alfaro *et al.*, 2005).

Exploring the intraspecific space of forms and functions and linking it to an agronomic trait space using model crop species has several advantages. From a theoretical standpoint, analysing the functional trait space of crops allows to investigate evolutionary issues by assessing the impact of artificial selection on trait covariations, their overall flexibility or robustness. Some evidence suggests that intraspecific trait covariations were weakened in crops (Martin & Isaac, 2015; Martin *et al.*, 2017). This may result in fewer correlations between traits at the whole plant scale, especially between root and leaf traits (Milla *et al.*, 2014; Isaac *et al.*, 2017; Roucou *et al.*, 2018), compared to wild species. This could be due to different selection pressures in crops compared to wild species (Milla *et al.*, 2014, 2015; Cantarel *et al.*, 2020), or because crop species have narrower phenotypic variation associated with narrower phylogenetic scales (Messier *et al.*, 2017; McCormack *et al.*, 2020). From an applied perspective, identifying proxies of agronomic performance is a long-standing objective for plant breeders (e.g. McClean *et al.*, 2011). The conceptual thinking of crop ideotypes (Donald, 1968), which seeks combinations of plant traits that contribute to increased yield at high planting densities, has enabled targeted efforts to improve light acquisition and use through aerial ideotype selection (Donald, 1968), and more recently the development of root ideotypes (York *et al.*, 2013; Lynch, 2013). These approaches demonstrated that different phenotypes, in terms of root anatomy, morphology and architecture, enhance the production in harsh environments (Lynch, 1995; Watt *et al.*, 2006; York *et al.*, 2013). The existence of multiple trait covariations is a well-known obstacle to identifying proxies of crop performance, particularly when biophysical constraints are at play (Annicchiarico & Pecetti, 1998; Yuan *et al.*, 2011; Chairi *et al.*, 2020). Yet, applying functional trait-based approaches, especially when considering the entire phenotype encompassing above- and belowground compartments, holds promise in addressing this issue.

In this study, we investigated intraspecific covariations of above- and below-ground traits and agronomic traits measured in the field for 179 genetically and phenotypically diverse inbred lines. These lines represented a highly diversified evolutionary pre-breeding population (EPO) founded with wild, primitive, and cultivated elite subspecies of durum wheat (David *et al.*, 2014). Firstly, we tested whether the intraspecific functional space of durum wheat is structured by the same trade-offs as those observed at the interspecific level. We hypothesised that the structure of the durum wheat functional space would differ from the well-known interspecific space, as crop species evolution has been strongly driven by artificial selection and by local adaptation to artificial

environments. Secondly, we tested whether and how artificial selection has impacted the structure of functional and agronomic trait space. We hypothesised that artificial selection has led to changes in trait covariations, due to selection pressures that have potentially restricted phenotypic variation and weakened trait-trait relationships. Lastly, we tested whether functional traits (or trait combinations) were related to agronomic traits. We expected that genotypes' functional trait values, which were used as proxies for functional strategies, would be good predictors of the observed agronomic traits, as suggested by the trait-to-performance mapping framework in trait-based ecology (Arnold, 1983; Violle *et al.*, 2007).

V. Materials and Methods

Plant material and experimental design

We grew 179 inbred lines of *Triticum turgidum ssp. durum* (Desf.) Husn. derived from a highly diversified evolutionary pre-breeding population in the field at Mauguio, southern France (INRAE – UE DIASCOPE – 43°36'N, 3°59'E). The EPO population was developed through crosses between different compartments of durum wheat's domestication history, ranging from wild and primitive *Triticum turgidum* subspecies to elite genotypes (David *et al.*, 2014). The set of EPO lines is a relevant material to test our questions because it captures a substantial amount of genetic and phenotypic variability of the *Triticum turgidum* subspecies. We set up the field experiment on November 21, 2017. Each of the 179 inbred lines was cultivated in randomly arranged single-genotype plots. The plots had dimensions of 1.5 m by 1.2 m and consisted of six rows each measuring 1.5 meters in length. There was a spacing of 20cm between rows and 2-3 cm between plants within the same row, resulting in a planting density of 240 plants per square meter. The plots were separated by 30 cm horizontally and 2 m vertically. (see Fig.1 in Montazeaud *et al.*, 2020b). The soil at the experimental site was stony loam, with about 1% organic matter and a pH of 8.7. Nitrogen fertilization was applied twice during the wheat growth cycle with a rate of 109 kg ha⁻¹ and 87 kg ha⁻¹ of Nexen®. To protect against biotic damages, one herbicide (Pointer®UltraSX® (30 g ha⁻¹)), one graminicide (Auzon®Duo (1L ha⁻¹)), one insecticide (Karate®Xflow (0.063 L ha⁻¹)) treatments and two fungicides treatments (Priori®Xtra (1 L.ha⁻¹)) were applied during wheat growth cycle.

Measurement of functional traits

For a comprehensive comparison between intra- and interspecific patterns, we focused on measuring plant functional traits that have been widely studied on global studies (Díaz *et al.*, 2016; Weigelt *et al.*, 2021), and known to describe plant ecological strategies. Plant height (cm) was measured on three plants per plot at plant maturity. The heading date was defined as the date at which spikes become visible in 50% of the plants within a plot. We converted the observed dates into degree days by summing the daily average temperatures since sowing using a 0°C base temperature. One foliar disc with a diameter of 6 mm was collected on four healthy and mature leaves from randomly sampled individuals. The four discs of known area were dried together for a minimum of 48 hours at 60°C and then weighted in order to estimate the leaf mass per area (LMA, kg m⁻²). Additionally, the leaf nitrogen content (LNC, %) was estimated using spectral reflectance measurements of the foliar disc obtained with a LabSpec® 4 spectrometer and in-house calibration (Ecarnot *et al.*, 2013) (see also Supplementary information in Montazeaud *et al.*, 2020b for more details).

At the end of the tillering stage, a key stage for cereals, explaining a large part of variation in performance traits among plants (e.g., Xie *et al.*, 2016), two soil cores (10 cm diameter and 15 cm depth) with three to five plants, according to their distribution along the row, were collected for each line. Due to the gravitropism of durum wheat, few roots of the central plant of each soil core were cut during the process of soil sampling, allowing us to select well-developed entire roots connected to the plants. Roots connected to the central plant of the soil core were selected for trait measurements. Roots cut by the soil corer were not measured. Then, the roots were separated into seminal roots and adventitious roots. We focused solely on adventitious roots since they were the youngest and well-developed roots with no sign of senescence. In addition, they were produced at the same time as the production of the leaves on which the traits were measured, making it possible to test the covariations between root and leaf traits. By considering a single type of roots instead of a mixed root system, we were able to compare trait values across different genotypes, irrespective of their relative investment in root types (seminal or adventitious in this case). Root angle (RA) was measured at maturity between the two most distant adventitious roots (see also Supplementary information of Montazeaud *et al.*, 2020b). The collected roots were stained with methyl violet and scanned at a resolution of 800 dpi (EPSON EXPRESSION 1680). The root scans were analysed using WinRHIZO (pro Version 2009; Regent Instrument) software to estimate various traits for

each sample, including the number of root tips, the distribution of root lengths across different diameter classes, and the total root length and volume. Root subsamples and the remaining roots were then dried separately for at least 48 hours at 60°C. Mean root diameter (RD, mm) was calculated as the average of the median root diameters of each diameter class, weighted by the root length of each class. Specific root length (SRL, m g⁻¹) was calculated as the ratio of the total length of the sample divided by its dry mass. We estimated root tissue density (RTD, g cm⁻³) as the ratio of the dry mass divided by the root volume of the subsample and root branching intensity (RBI) as the ratio of the number of root tips in the subsample divided by its length. Root length density (RLD, cm cm⁻³) was computed by dividing the total root length by the soil core volume.

Measurement of agronomic traits

To link functional traits to genotype's agronomic performance, we measured six major agronomic traits at the plot level: vegetative biomass yield, grain yield, total biomass yield, thousand kernel weight, harvest index and seed number per m². At maturity, we harvested the aboveground biomass from the four central rows of each plot, covering a length of 70 cm, while leaving 40 cm on each side of the rows to minimize edge effects. Vegetative (leaves and stems) and reproductive (spikes with grains) biomasses were separated, dried and weighted. The spikes were threshed, and grains were weighted. Grain biomass was used to calculate grain yield (GY, g m⁻²). Vegetative biomass was used to estimate vegetative biomass yield per unit area (BY, g m⁻²). We computed the total biomass yield (TBY in g m⁻²) by summing the biomasses of grains, spikes and vegetative organs. The thousand kernel weight (TKW, g) was estimated by counting and weighting 250 grains per line. We calculated the harvest index as the ratio of the grain biomass divided by the total aboveground biomass (vegetative and reproductive), in order to evaluate whether genotypes with equal biomass invest more in grain or in vegetative biomass. Furthermore, we assessed the number of grains produced per unit area by calculating the ratio of grain biomass to the thousand kernel weight (seed number per m², Seed nb).

Assessing the degree of artificial selection based on genetic distance

EPO lines derived by successive selfing from a pre-breeding population originated from crosses between different genetic compartments of durum wheat, including wild and primitive *Triticum turgidum* subspecies and elite genotypes. Because the elite compartment has been strongly shaped through human selection, we hypothesised that for each EPO line, the lower the genetic distance

to the elite compartment, the stronger the artificial selection. We thus used genetic distance as a proxy of the degree of artificial selection for each EPO line. We estimated the genetic distance to elite lines by computing the average genetic distance of each EPO line to a common set of eight durum wheat elite varieties (Table S1) using 50,000 SNPs obtained from the TaBW280K high throughput genotyping array (Rimbert *et al.*, 2018). First, the SNPs matrix was converted into a *genind* object (*df2genind()* function, *adegenet* package), where each column represents a locus and each row a genotype. Next, we estimated the genetic distance as the average allelic differences with the elite compartment (calculated by averaging the allelic differences from the eight elites for each of the 179 genotypes), using the *diss.dist()* function of the *poppr* package.

Statistical analyses

All statistical analyses were performed with R version 4.1.0 (R Core Team, 2021).

To assess the structure of the intraspecific functional space of durum wheat, we performed a principal component analyses (PCA) based on aboveground (Height, LMA, LNC, Heading date) and belowground (RA, RBI, RD, RTD, RLD and SRL) traits (functional trait space hereafter), using the *PCA()* function of the *FactoMineR* package. A second PCA was performed on agronomic traits (BY, GY, Harvest index, Seed nb, TBY and TKW) (agronomic trait space hereafter). To determine the number of dimensions to retain in the PCAs, we employed the approach developed by Mouillot *et al.* (2021) based on the elbow inflection point for the area under the curve (AUC) criteria and the mean absolute deviation (MAD) (Fig. S1). The elbow method is based on the maximisation of a given benefit (AUC or MAD gain) while minimizing the cost (number of dimensions). To estimate the occurrence probability of given combinations of trait values in the multidimensional spaces, we used a two-dimensional kernel density estimation using the *kde()* function from the *ks* package. Detailed information on kernel density estimation is provided in Díaz *et al.* (2016).

We performed regression models to quantify the relationships between the genetic distance to elite compartment and the principal components of functional trait and agronomic trait spaces using the *lm()* function. We reported the coefficient of determination, R^2 (adjusted R-squared) for each model, as well as the 95% confidence level intervals for the model predictions computed as ± 1.96 unconditional sampling standard deviation (Burnham & Anderson, 1998).

To quantify the relationships between major agronomic traits, i.e. biomass yield, grain yield, harvest index, TKW, total biomass yield and seed number per m², and functional traits, we fitted for each agronomic trait a full model including all the functional traits and their quadratic terms, as explanatory variables (*lm()* function). We used quadratic terms to test whether various trait values could lead to similar agronomic performance (several peaks in agronomic performance; illustrating a “many-to-one mapping” between traits and performance). Both the dependent and independent variables were standardized ($\mu = 0$, $\sigma = 1$). We then performed a backward model selection (*glmulti()* function from the *glmulti* package) to rank the models according to their Akaike Information Criterion values, corrected for small sample size (Sugiura, 1978; Burnham & Anderson, 1998), and we selected the N best models with AICc differences from the first model lower than two (Table S2, S3, S4, S5). We then conducted model-averaging, based on the N best models, using the *coef()* function from *glmulti* package in order to obtain standardized parameter estimates and their 95% unconditional confidence intervals, as well as trait relative importance and adjusted R-squared.

VI. Results

Functional and agronomic trait spaces occupied by durum wheat lines

The four principal components (PC) that structure the functional trait space explained 66% of the variability. The first two principal components, PC1 and PC2, altogether explained 42% of the variability (Fig. 1a; Fig. S1). PC1 (24.2%) was strongly positively associated with RD and RBI, while negatively correlated with SRL and RLD (Fig. 1a). This component represents a gradient from genotypes that extensively explore the soil with fine, long and sparsely branched roots to genotypes that invest in thicker, more branched roots (left to right in Fig. 1a; Table S6). PC2 explained 17.8% of the variability. It was positively associated with LNC and SRL, while negatively associated with RTD and LMA (Fig. 1a; Table S6). PC2 represents a gradient from genotypes with dense tissues to genotypes with low density tissues, high nitrogen content and high SRL values. PC3 explained 12.7% of the variability, and was positively correlated with RTD, RA and Heading date. PC4, explaining 11.3% of the variability, was positively associated with plant height and RLD and negatively associated with RA (Fig. S2; Table S6).

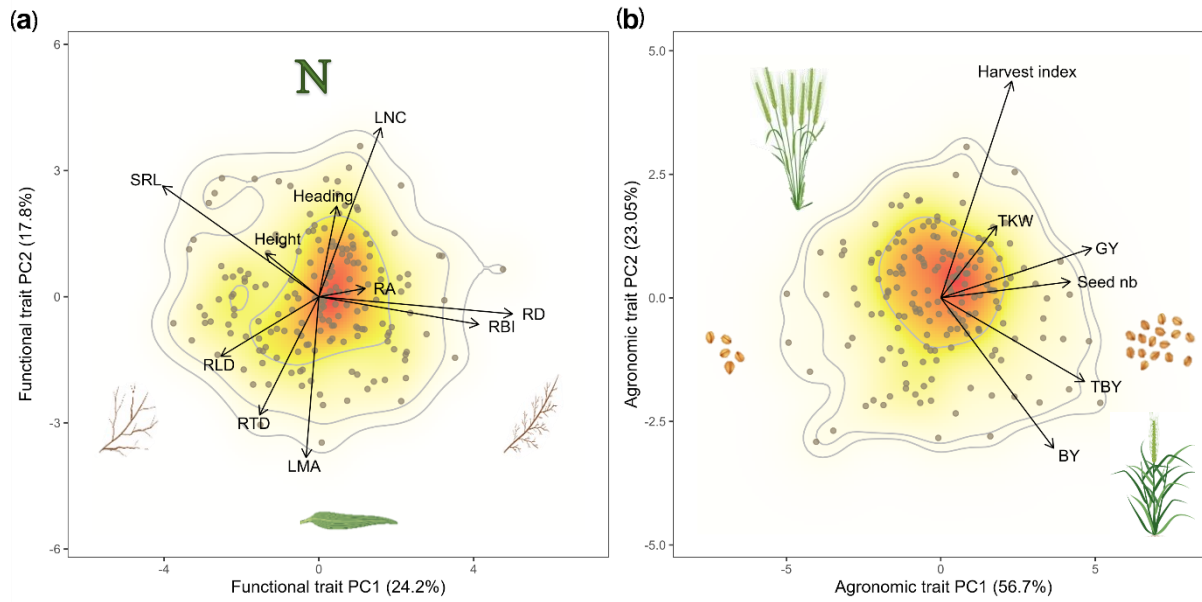


Fig. 1 Projection of the 179 durum wheat lines (*Triticum turgidum* spp. *durum*) on the plane defined by the first two components of a principal component analysis based on: (a) above- and belowground functional traits: Heading (degree days): Heading date; Height (cm): maximal plant height, LMA (kg m^{-2}): Leaf mass area; LNC (%): Leaf nitrogen content; RA ($^{\circ}$): Root angle; RBI (number of tips per length unit): Root branching intensity; RD (mm): Root diameter; RLD (cm cm^{-3}): Root length density; RTD (g cm^{-3}): Root tissue density and SRL (m g^{-1}): Specific root length; (b) agronomic traits related to biomass production and reproduction: BY (g m^{-2}): Biomass yield; GY (g m^{-2}): Grain yield; Harvest index: Harvest index; Seed nb: Seed number per m^2 ; TBY (g m^{-2}): Total biomass yield; TKW (g): Thousand kernel weight. The colour gradient and contour lines correspond to the 0.5, 0.95 and 0.99 quantiles of the respective probability distribution, thus highlighting the regions of highest (orange) and lowest (white) trait value combination occurrence probability.

Three principal components characterized the agronomic trait space of the 179 genotypes and accounted for 98% of the variability (Fig. 1b; Fig. S1; Table S6). PC1 (56.7%) was mainly correlated with grain production, while PC2 (23.05%) was correlated with vegetative biomass. PC1 was positively associated with grain yield and total biomass yield (GY and TBY) as well as seed number per m^2 . PC2 was highly positively associated with harvest index and negatively with biomass yield (BY) (Fig. 1b; Table S6). PC3 was positively associated with thousand kernel weight and negatively with the number of seeds per m^2 (Fig. S2; Table S6).

Footprint of artificial selection on the functional and agronomic trait spaces

We detected no significant relationship between PC1 and PC2 of the functional trait space and the genetic distance between EPO lines and the elite durum wheat compartment ($p > 0.05$, Fig. 2a, b). Conversely, the first two PCs of the agronomic trait space were both negatively correlated with the genetic distance ($R^2 = 0.03$, $p = 0.01$; $R^2 = 0.05$, $p = 0.001$, respectively; Fig. 2c, d). Thus, the smaller the genetic distance between an EPO line and the elite compartment, the higher its grain yield, total biomass yield and number of seeds per m^2 (Fig. 2c), the lower its biomass yield, and the greater its harvest index (Fig. 2d). PC3 of the agronomic trait space did not significantly covary with genetic distance ($p > 0.05$, Fig. S3c).

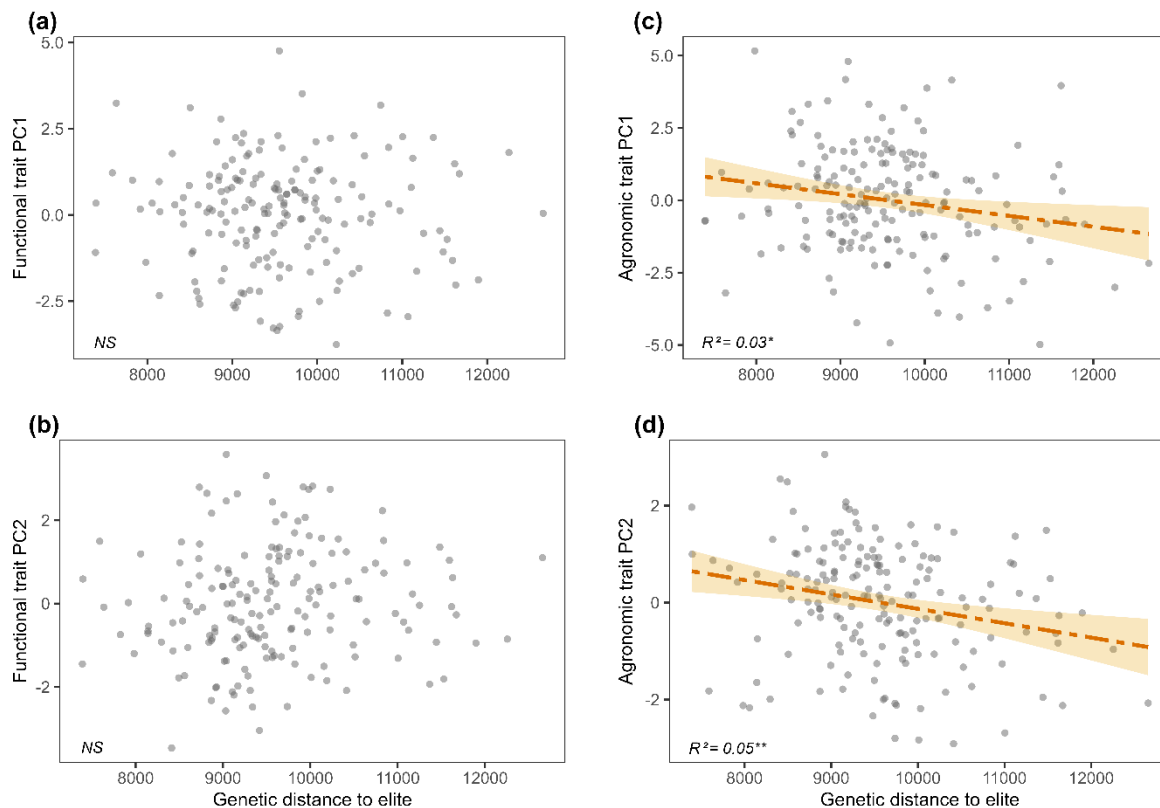


Fig. 2 Relationships between the degree of artificial selection of durum wheat genotypes, *Triticum turgidum* ssp. durum, (assessed by the genetic distance to elite compartment) and the two first components of the functional trait space (a), (b) and agronomic trait space (c), (d). For each relationship, the adjusted coefficient of determination R^2 is given. Significance: NS, not significant; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. The red dotted line shows the predicted relationship by the model with the 95% confidence level interval in orange.

The functional trait-to-agronomic performance mapping

The adjusted mean R-squared of the best full models for each agronomic trait ranged from 0.08 for the seed number per m² to 0.31 for biomass yield. Total biomass yield, grain yield, thousand kernel weight and harvest index had intermediate values with R-squared of 0.11, 0.15, 0.22 and 0.25 respectively (Fig. 3; Fig. S4; Table S2, S3, S4, S5). We found that functional traits better explained agronomic performance when pooled in the analysis (R^2 ranging from 0.15 to 0.31; Fig. 3) than when analysed individually (R^2 ranging from 0.02 to 0.20; Fig. 4). Several functional traits, both aboveground and belowground traits, had jointly a significant relationship with agronomic traits (Fig. 3; Fig. 4). Biomass yield was positively related to plant height, leaf nitrogen content, and to the root angle quadratic term, and negatively to the specific root length quadratic term, i.e., genotypes with higher vegetative biomass production were tall with high leaf nitrogen content, intermediate SRL values and either very high or very low root angle values (Fig. 3a; Fig. 4a, b, c, d). Grain yield was jointly explained by LMA (quadratic term), heading date, root tissue density and root diameter (Fig. 3b). Additionally, harvest index was positively explained by LMA quadratic term and negatively by root diameter, heading date and height quadratic term (Fig. 3c). Investment in grain biomass was higher for early genotypes, with thinner roots and peaked for low or high LMA values (Fig. 3c; Fig. 4e, f, g, i, j, k). Thousand kernel weight was significantly associated to plant height, RTD (quadratic term), and root diameter (Fig. 3d). Genotypes with high thousand kernel weight values were tall genotypes, with thinner roots, and low or high RTD values (Fig. 3d; Fig. 4m, n, o). The functional traits that had the broadest effect on agronomic traits were not always the ones that contributed the most to the functional trait space structure (Fig. 1a); in particular, plant height and heading date (Fig. 4a, e, i, m), which mostly contributed to the third and fourth axes of variation (i.e., PC3 and PC4).

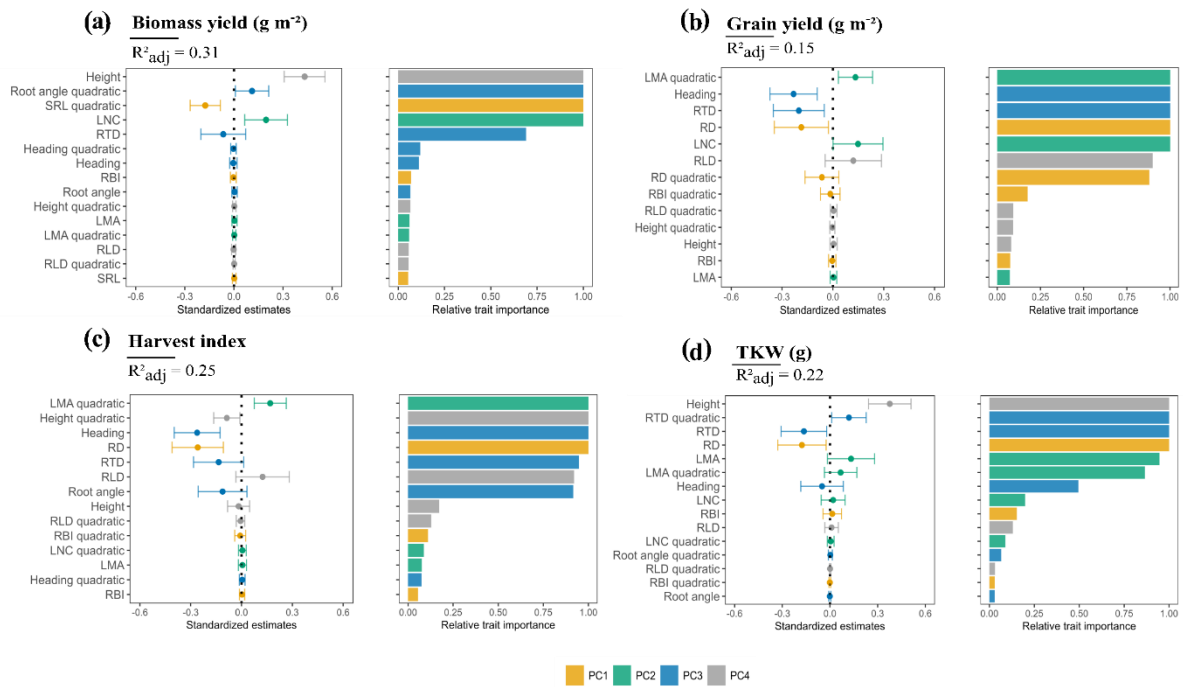


Fig. 3 Standardized effects of functional traits on agronomic traits including biomass yield (g m^{-2} , (a)), grain yield (g m^{-2} , (b)), harvest index (c) and thousand kernel weight (TKW, g, (d)). Above- and belowground functional traits: Heading date in degree days (Heading); Maximal plant height in cm (Height); Leaf mass area in kg m^{-2} (LMA); Leaf nitrogen content in % (LNC); Root angle ($^{\circ}$); Root branching intensity in number of tips per length unit (RBI); Root diameter in mm (RD); Root length density in cm cm^{-3} (RLD); Root tissue density in g cm^{-3} (RTD) and Specific root length in m g^{-1} (SRL). A quadratic term was added in the models to test non-linear relationships between functional traits and agronomic traits. Backward model selection was performed on a full model with agronomic traits as the response variable and all functional traits as explanatory variables (Table S2, S3, S4, S5). The N best models based on an AICc difference lower than two were retained to compute model-averaged estimates reported on the left side of the four panels with their 95% unconditional confidence intervals. The relative importance of functional traits is reported on the right side of the four panels and can be interpreted as the probability that the trait is in the best model. Although a functional trait is represented on several dimensions, we assigned colours to the dimensions of the functional trait space where the trait contributes most. Adjusted R-squared averaged across the N best models (R^2_{adj}) are also presented for the four models.

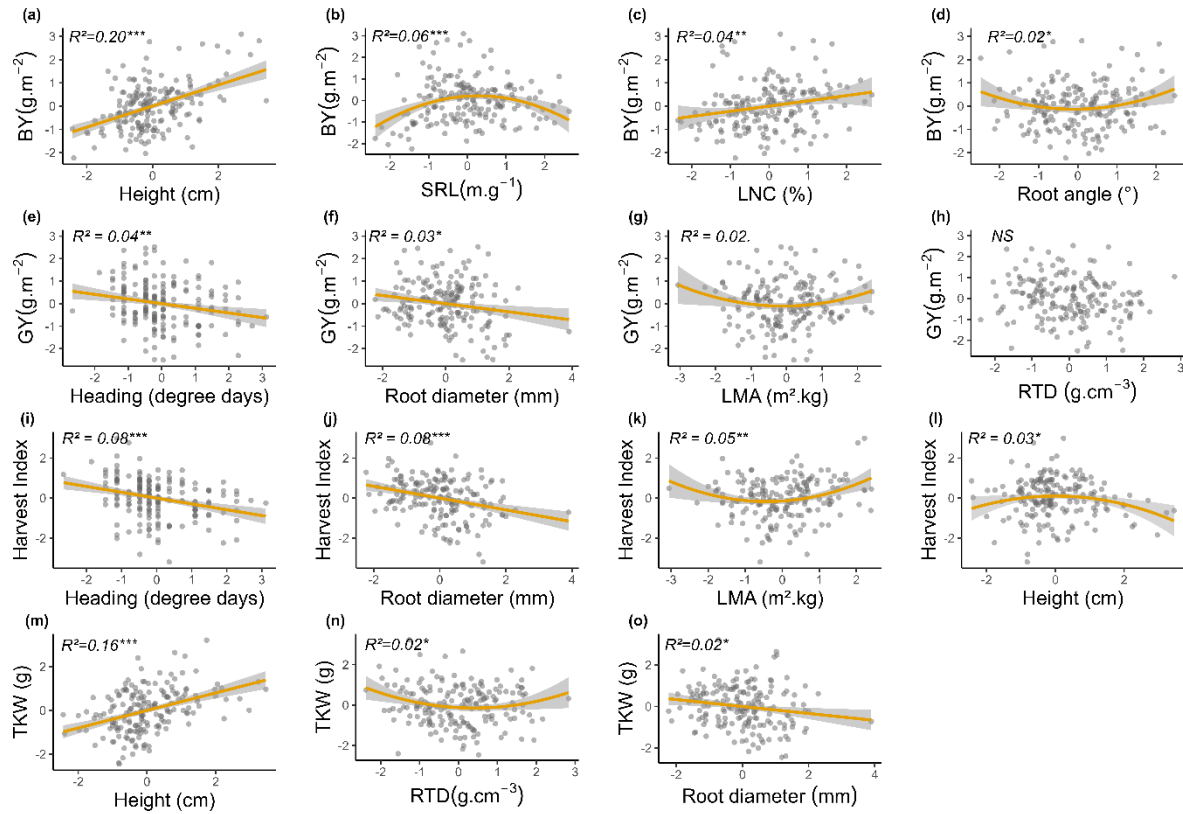


Fig. 4 Univariate relationships between the four agronomic traits and functional traits. Agronomic traits related to biomass production and reproduction: BY ($\text{g}\cdot\text{m}^{-2}$), Biomass yield; GY ($\text{g}\cdot\text{m}^{-2}$), Grain yield; Harvest index, Harvest index; TKW (g), Thousand kernel weight. Above- and belowground functional traits: Heading (degree days), Heading date; Height (cm), maximal plant height, LMA ($\text{kg}\cdot\text{m}^{-2}$), Leaf mass area; LNC (%), Leaf nitrogen content; Root angle ($^\circ$); Root diameter (mm); RTD ($\text{g}\cdot\text{cm}^{-3}$), Root tissue density and SRL ($\text{m}\cdot\text{g}^{-1}$), Specific root length. Functional traits shown had the highest relative importance (i.e. they were selected by all the N best models; Fig. 3) and had standardized estimates with 95% unconditional confidence intervals that did not cross 0. For each relationship, the adjusted coefficient of determination R^2 is given. Significance: NS, not significant; $P \sim 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. The red solid line shows the predicted relationship by the model with the 95% confidence level interval in orange.

VII. Discussion

In this study, using 179 durum wheat genotypes, we demonstrated that intraspecific trait covariations are structured by the same trade-offs than those previously described at the interspecific level (Westoby *et al.*, 2002; Wright *et al.*, 2004; Reich, 2014; Díaz *et al.*, 2016;

Weigelt *et al.*, 2021). We did not detect any effect of artificial selection on the genotype position within this functional space, whereas we found a strong footprint of artificial selection on the agronomic space, confirming the strong impact of human selection on yield-related traits. Our findings also revealed that combinations of above- and belowground traits explained wheat performance at the plot level, which both enriches our understanding on the relationship between genotype functional traits and their performance outcomes (Wainwright *et al.*, 2005; Violle *et al.*, 2007) and brings insightful information for multi-criteria yield improvement (Arnold, 1983; Annicchiarico & Pecetti, 1998).

A fundamental question in functional ecology is whether trait covariations are maintained both among species and within species (Vasseur *et al.*, 2012; Shoval *et al.*, 2012; Niinemets, 2015; Isaac *et al.*, 2017; Messier *et al.*, 2017; Sartori *et al.*, 2019). By considering both above- and belowground traits, we provide evidence that the intraspecific functional space of durum wheat is structured by the same trade-offs than those observed at the interspecific level (Díaz *et al.*, 2016; Weigelt *et al.*, 2021). Root traits played a significant role in shaping the phenotypic space, particularly in supporting the two main axes of trait covariation. The first axis opposed specific root length and root diameter. This axis is commonly described as a gradient of soil exploration strategies, contrasting genotypes that are efficient at exploring the soil and acquiring resources thanks to their ability to develop fine and economical roots, to thick-rooted genotypes that invest more carbon in soil exploration and may rely more on mycorrhizal partnerships for resource acquisition (Eissenstat *et al.*, 2015; Kramer-Walter *et al.*, 2016; Bergmann & Weigelt, 2020; Weigelt *et al.*, 2021). In this study, this axis is also associated to the root branching intensity, which positively covaried with root diameter. Thick roots are more densely branched than thin roots; this suggests that genotypes with high specific root length values extensively explore the soil by producing long, thin roots with few ramifications, while thick-rooted genotypes achieve intensive soil exploration through high branching, potentially enhancing their ability to exploit nutrient-rich patches (Hodge, 2004; Kong *et al.*, 2014). This finding contradicts expectations based on trees studies (Eissenstat *et al.*, 2015; Liese *et al.*, 2017) and rice research (Montazeaud *et al.*, 2018), i.e., thicker root are usually found to be more sparsely branched. As with many other root traits (e.g., root hairs, exudates), this emphasizes that we lack knowledge about root constraints that shape genotype position within the phenotypic space, despite the acknowledged importance of roots for resource acquisition (York *et al.*, 2013). The second axis of trait covariation can be associated with

the well-documented trade-off between ‘fast’ and ‘slow’ return on carbon and nutrient investment (Reich, 2014). This axis opposes genotypes with dense root tissue and high leaf mass per area values to those with high leaf nitrogen content. This result supports the idea that the ‘fast-slow’ trade-off is common for both above- and belowground organs (Weigelt *et al.*, 2021), and that similar trade-offs shape plant phenotypic space at both inter- and intra-specific level, even within a crop species. These findings emphasize the importance of further investigating intraspecific variation in root traits, considering their crucial role in determining key physiological and ecological plant strategies across different environments (Borden *et al.*, 2020; Freschet *et al.*, 2021; Weemstra *et al.*, 2021).

In addition to the commonalities observed between the wheat functional space and interspecific spaces described in functional ecology, we highlighted peculiarities that can be attributed to the life history of durum wheat, notably the breeding history of EPO lines. Unlike the study of Díaz *et al.* (2016), in which the first axes of variation depict a size gradient, here variation in plant height was not well described by the two major axes of the functional space. This discrepancy between patterns of variation in natural populations and those observed in our study could be explained by the fact that plant height variability has been reduced through the selection of durum wheat. Reduced stature has been strongly favoured since the Green Revolution to prevent lodging in nitrogen-rich conditions and to limit plant competition for light (Donald, 1968; Peng *et al.*, 2011; Montazeaud *et al.*, 2020a). Because of its breeding history (David *et al.*, 2014; Montazeaud *et al.*, 2020b), height variability in EPO remains higher than in modern durum wheat and we expected this height variability to further shape the phenotypic space of this species, but our findings did not support this expectation. The third variation axis was phenology-driven, where late heading was associated with high carbon-based construction costs, as indicated by high root tissue density, highlighting the existence of another component that may be related to the ‘fast-slow’ continuum. This finding underscores the significant role of phenology in crop physiology and justifies its long history of selection in agronomy (e.g., Jung & Müller, 2009). Conversely, phenology has been poorly integrated in interspecific functional spaces so far (but see Segrestin *et al.*, 2018). Beyond the well-known key role of phenology in annual plants (see e.g., Sartori *et al.*, 2019), a more systematic integration of phenological traits in large-scale interspecific analyses is a priority for the research field.

Several studies have shown that domesticated species tend to have faster growth and more ‘fast’ resource use strategies than their wild relatives (Hancock, 2012; Milla *et al.*, 2015; Milla & Matesanz, 2017; Roucou *et al.*, 2018; Isaac *et al.*, 2021), which is interpreted as an adaptation to nutrient-rich habitats (Chapin, 1980; Pujol *et al.*, 2008; Milla *et al.*, 2014; Roucou *et al.*, 2018). Here, variation in functional traits was not explained by the genetic distance of EPO genotypes to modern varieties, which can be interpreted as a lack of effect of artificial selection on the positioning of genotypes within the phenotypic space, suggesting that trade-offs between traits are difficult to overcome. However, we cannot ignore a potential bias in our quantification of the degree of artificial selection that has been inferred on the whole-genome level while only a reduced number of genes probably capture human-driven selection (Doebley *et al.*, 2006). On the opposite, we found significant relationships between the different facets of wheat’s agronomic performance and the degree of artificial selection. As expected, genotypes that shared more genetic similarities with modern varieties displayed higher values of harvest index, total biomass and grain production, and lower values of vegetative biomass. This could be explained by the fact that artificial selection has deliberately acted on yield components in the evolutionary history of crops (Harlan *et al.*, 1973; Hay, 1995; Peng *et al.*, 2011; Peleg *et al.*, 2011). Due to the absence of a significant effect of genetic distance to modern varieties on durum wheat functional traits that are indirectly linked to agronomic performance, we hypothesise that these traits could serve as promising candidates for future breeding programs aimed at better adapting varieties to constraints of new environments.

According to Arnold's (1983) paradigm, later adapted in functional ecology (Violle *et al.*, 2007), functional traits are expected to influence directly and indirectly plant fitness. The multifaceted nature of resource-use strategies and plant performance has long impeded a comprehensive evaluation of the functional traits-to-performance mapping in both wild and crop species (Phillips & Arnold, 1989; Laughlin & Messier, 2015). The complexity of trait-performance relationships stems from the multivariate nature of plant phenotypes, where traits are interrelated throughout the plant. For example, if a trait A has a positive effect on genotype performance, this effect can in fact be due to the effect of a trait B that interacted with A (Phillips & Arnold, 1989). Here, we identified above- and belowground traits combinations that were related to agronomic performance, thus confirming that trait-performance mapping is multidimensional. Although these combinations of functional traits explain a limited part of the variation for some agronomic traits, it is noteworthy that functional traits from the fourth PC axis of the durum wheat phenotypic space

are involved in these relationships, which underlines the fact that agronomic performances are dependent on the whole plant phenotype. Despite not being well described by the first two axes of the phenotypic space, plant height and heading date were strongly associated with agronomic performance. Tall genotypes produced higher amounts of vegetative biomass and heavier grains, but did not necessarily produce the greatest amount of grains, in part because of the quadratic relationship between plant height and harvest index. In parallel, heading date was negatively related to harvest index and grain yield. As a result, early heading genotypes with an intermediate plant height had higher harvest index and grain yield. Plant height and crop phenology jointly strongly influence the yield of crops, as previously described in rice crops (Li *et al.*, 2012), in wheat (Hyles *et al.*, 2020) and oat (Rosielle & Frey, 1975), in particular because these traits are strongly involved in plant responses to abiotic and biotic factors and therefore influence allocation patterns within the plant (Donald & Hamblin, 1976; Hill & Li, 2016). Simultaneously, traits associated with the ‘fast-slow’ economic spectrum also played a significant role in explaining agronomic performances: mid-spectrum genotypes (displaying intermediate LNC, LMA and RTD) produced less vegetative biomass and grain biomass than ‘fast’ genotypes, which produced higher vegetative biomass and heavier seeds. Moreover, root systems characterized by high specific root length, high root length density and low root diameter can facilitate belowground resource foraging (e.g., Campbell *et al.*, 1991; Freschet *et al.*, 2021), which could in turn increase the allocation of resources to the growth and reproductive function. We found in particular a maximization of biomass yield at intermediate values of specific root length. These findings support the links between root traits, resource acquisition strategies and yield components and underpin the importance of an underground ideotype for crop improvement (Richardson *et al.*, 2011; York *et al.*, 2013; Lynch, 2013).

Our findings call for mobilizing breeding approaches that consider multidimensional phenotypic space to take into account plant trade-offs and potentially even override them (Denison, 2015; Isaac & Martin, 2019; Rolhauser *et al.*, 2022). The existence of multiple phenotypic pathways to plot-level performances opens new avenues for plant breeding programs since several traits should be targeted simultaneously. Multi-criteria crop breeding has made a lot of progress in recent years though (Cabrera-Bosquet *et al.*, 2012; Moeinizade *et al.*, 2020), and we are confident that future fruitful interactions between ecology and agronomy will lead to better identification of breeding targets and to the removal of still largely unknown phenotypic and genetic constraints.

VIII. Acknowledgements

Experimental work was supported by the European Research Council (ERC) Starting Grant Project ‘Ecophysiological and biophysical constraints on domestication in crop plants’ (Grant ERC-StG-2014-639706CONSTRAINTS) and by the project ‘Supporting Agrobiodiversity in Mediterranean Agroecosystems to improve Drought Adaptation’ (SAADA), an Open Science project of Agropolis Fondation. We thank the DIASCOPE platform (INRAE, Mauguio, FRANCE), and the PACE platform (technical facilities of the Labex Centre Méditerranéen de l'Environnement et de la Biodiversité, CEMEB, Montpellier, FRANCE) for providing all the facilities and technical support. We also acknowledge Eric Antoine Gonzalez (University of Clemson) for copyediting this paper. TL is funded by the Agence Nationale de la Recherche (ANR) project “Selecting for cooperative crops to develop sustainable agriculture” (SCOOP, grant no. ANR-19-CE32-0011).

IX. Author contributions

CV, FF, and HF planned and designed the research. GM, AR, FF and HF performed the experiment. TL analysed the data. TL, CV and FF wrote the first version of the manuscript, with inputs from GM, HF and MI. All authors read and approved the final manuscript.

X. Data availability

The data to reproduce all analyses of this paper can be accessed at <https://osf.io/23vfe/>.

XI. References

Ackerly DD, Dudley SA, Sultan SE, Schmitt J, Coleman JS, Linder CR, Sandquist DR, Geber MA, Evans AS, Dawson TE, et al. 2000. The Evolution of Plant Ecophysiological Traits: Recent Advances and Future Directions. *BioScience* **50**: 979.

Adler PB, Salguero-Gómez R, Compagnoni A, Hsu JS, Ray-Mukherjee J, Mbeau-Ache C, Franco M. 2014. Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences* **111**: 740–745.

- Alfaro ME, Bolnick DI, Wainwright PC. 2005.** Evolutionary Consequences of Many-to-One Mapping of Jaw Morphology to Mechanics in Labrid Fishes. *The American Naturalist* **165**: E140–E154.
- Annicchiarico P, Pecetti L. 1998.** Yield vs. morphophysiological trait-based criteria for selection of durum wheat in a semi-arid Mediterranean region (northern Syria). *Field Crops Research* **59**: 163–173.
- Arnold SJ. 1983.** Morphology, Performance and Fitness. *American Zoologist* **23**: 347–361.
- Barton N, Partridge L. 2000.** Limits to natural selection. *BioEssays* **22**: 1075–1084.
- Bergmann J, Weigelt A. 2020.** The fungal collaboration gradient dominates the root economics space in plants. *Science Advances* **6**: 37–56.
- Borden KA, Anglaaere LCN, Owusu S, Martin AR, Buchanan SW, Addo-Danso SD, Isaac ME. 2020.** Soil texture moderates root functional traits in agroforestry systems across a climatic gradient. *Agriculture, Ecosystems & Environment* **295**: 106915.
- Bulman P, Hunt LA. 1988.** Relationships among tillering, spike number and grain yield in winter wheat (*Triticum aestivum* L.) in Ontario. *Canadian Journal of Plant Science* **68**: 583–596.
- Burnham KP, Anderson DR. 1998.** Practical use of the information-theoretic approach. In: Model selection and inference. New-York, NY: Springer, 75–117.
- Cabrera-Bosquet L, Crossa J, von Zitzewitz J, Serret MD, Luis Araus J. 2012.** High-throughput Phenotyping and Genomic Selection: The Frontiers of Crop Breeding Converge. *Journal of Integrative Plant Biology* **54**: 312–320.
- Campbell BD, Grime JP, Mackey JML. 1991.** A trade-off between scale and precision in resource foraging. *Oecologia* **87**: 532–538.
- Cantarel AAM, Allard V, Andrieu B, Barot S, Enjalbert J, Gervais J, Goldringer I, Pommier T, Saint-Jean S, Le Roux X. 2020.** Plant functional trait variability and trait syndromes among wheat varieties: the footprint of artificial selection. *Journal of Experimental Botany*.
- Chairi F, Sanchez-Bragado R, Serret MD, Aparicio N, Nieto-Taladriz MT, Luis Araus J. 2020.** Agronomic and physiological traits related to the genetic advance of semi-dwarf durum wheat: The case of Spain. *Plant Science* **295**: 110210.
- Chapin FS. 1980.** The Mineral Nutrition of Wild Plants. *Annual Review of Ecology and Systematics* **11**: 233–260.
- David J, Holtz Y, Ranwez V, Santoni S, Sarah G, Ardisson M, Poux G, Choulet F, Genthon C, Roumet P, et al. 2014.** Genotyping by sequencing transcriptomes in an evolutionary pre-breeding durum wheat population. *Molecular Breeding* **34**: 1531–1548.
- Denison RF. 2015.** Evolutionary tradeoffs as opportunities to improve yield potential. *Field Crops Research* **182**: 3–8.
- Diaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, Montserrat-Martí G, Grime JP, Zarrinkamar F, Asri Y, et al. 2004.** The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science* **15**: 295–304.

- Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Colin Prentice I, et al. 2016.** The global spectrum of plant form and function. *Nature* **529**: 167–171.
- Doebley JF, Gaut BS, Smith BD. 2006.** The Molecular Genetics of Crop Domestication. *Cell* **127**: 1309–1321.
- Donald CM. 1968.** The breeding of crop ideotypes. *Euphytica* **17**: 385–403.
- Donald CM, Hamblin J. 1976.** The Biological Yield and Harvest Index of Cereals as Agronomic and Plant Breeding Criteria. In: Brady NC, ed. *Advances in Agronomy*. Academic Press, 361–405.
- Donovan LA, Maherali H, Caruso CM, Huber H, de Kroon H. 2011.** The evolution of the worldwide leaf economics spectrum. *Trends in Ecology & Evolution* **26**: 88–95.
- Ecarnot M, Compan F, Roumet P. 2013.** Assessing leaf nitrogen content and leaf mass per unit area of wheat in the field throughout plant cycle with a portable spectrometer. *Field Crops Research* **140**: 44–50.
- Eissenstat DM, Kucharski JM, Zadworny M, Adams TS, Koide RT. 2015.** Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest. *New Phytologist* **208**: 114–124.
- Freschet GT, Roumet C, Comas LH, Weemstra M, Bengough AG, Rewald B, Bardgett RD, De Deyn GB, Johnson D, Klimešová J, et al. 2021.** Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. *New Phytologist*: nph.17072.
- Garland T, Downs CJ, Ives AR. 2022.** Trade-Offs (and Constraints) in Organismal Biology. *Physiological and Biochemical Zoology* **95**: 82–112.
- Garnier E, Navas M-L, Grigulis K. 2016.** *Plant Functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties*. Oxford, UK: Oxford University Press.
- Garnier E, Fayolle A, Navas M-L, Damgaard C, Cruz P, Hubert D, Richarte J, Autran P, Laurent C, Violle C. 2018.** Plant demographic and functional responses to management intensification: A long-term study in a Mediterranean rangeland. *Journal of Ecology* **106**: 1363–1376.
- Gould SJ, Lewontin RC, Maynard Smith J, Holliday R. 1997.** The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **205**: 581–598.
- Grime JP. 1977.** Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist* **111**: 1169–1194.
- Grubb PJ. 2016.** Trade-offs in interspecific comparisons in plant ecology and how plants overcome proposed constraints. *Plant Ecology & Diversity* **9**: 3–33.
- Hancock JF. 2012.** *Plant Evolution and the Origin of Crop Species*. Wallingford, UK: CABI.
- Harlan JR, de Wet JMJ, Price EG. 1973.** Comparative Evolution of Cereals. *Evolution* **27**: 311–325.
- Hay RKM. 1995.** Harvest index: a review of its use in plant breeding and crop physiology. *Annals of Applied Biology* **126**: 197–216.

Hill CB, Li C. 2016. Genetic Architecture of Flowering Phenology in Cereals and Opportunities for Crop Improvement. *Frontiers in Plant Science* **7**.

Hodge A. 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist* **162**: 9–24.

Hyles J, Bloomfield MT, Hunt JR, Trethowan RM, Trevaskis B. 2020. Phenology and related traits for wheat adaptation. *Heredity* **125**: 417–430.

Isaac ME, Martin AR, de Melo Virginio Filho E, Rapidel B, Roupsard O, Van den Meersche K. 2017. Intraspecific Trait Variation and Coordination: Root and Leaf Economics Spectra in Coffee across Environmental Gradients. *Frontiers in Plant Science* **8**.

Isaac ME, Martin AR. 2019. Accumulating crop functional trait data with citizen science. *Scientific Reports* **9**: 15715.

Isaac ME, Nimmo V, Gaudin ACM, Leptin A, Schmidt JE, Kallenbach CM, Martin A, Entz M, Carkner M, Rajcan I, et al. 2021. Crop Domestication, Root Trait Syndromes, and Soil Nutrient Acquisition in Organic Agroecosystems: A Systematic Review. *Frontiers in Sustainable Food Systems* **5**: 716480.

Jung C, Müller AE. 2009. Flowering time control and applications in plant breeding. *Trends in Plant Science* **14**: 563–573.

Koehl MAR. 1996. When does morphology matter? *Annual Review of Ecology and Systematics* **27**: 501–542.

Kong D, Ma C, Zhang Q, Li L, Chen X, Zeng H, Guo D. 2014. Leading dimensions in absorptive root trait variation across 96 subtropical forest species. *New Phytologist* **203**: 863–872.

Kozak M, Mađry W. 2006. Note on yield component analysis. *Cereal Research Communications* **34**: 933–940.

Kramer-Walter KR, Bellingham PJ, Millar TR, Smissen RD, Richardson SJ, Laughlin DC. 2016. Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology* **104**: 1299–1310.

Laughlin DC. 2014. The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology* **102**: 186–193.

Laughlin DC, Messier J. 2015. Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends in Ecology & Evolution* **30**: 487–496.

Laughlin DC, Gremer JR, Adler PB, Mitchell RM, Moore MM. 2020. The Net Effect of Functional Traits on Fitness. *Trends in Ecology & Evolution* **35**: 1037–1047.

Li X, Yan W, Agrama H, Jia L, Jackson A, Moldenhauer K, Yeater K, McClung A, Wu D. 2012. Unraveling the Complex Trait of Harvest Index with Association Mapping in Rice (*Oryza sativa* L.). *PLOS ONE* **7**: e29350.

- Liese R, Alings K, Meier IC. 2017.** Root Branching Is a Leading Root Trait of the Plant Economics Spectrum in Temperate Trees. *Frontiers in Plant Science* **8**: 315.
- Lynch J. 1995.** Root Architecture and Plant Productivity. *Plant Physiology* **109**: 7–13.
- Lynch JP. 2013.** Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. *Annals of Botany* **112**: 347–357.
- Marks CO, Lechowicz MJ. 2006.** Alternative Designs and the Evolution of Functional Diversity. *The American Naturalist* **167**: 55–66.
- Martin AR, Isaac ME. 2015.** REVIEW: Plant functional traits in agroecosystems: a blueprint for research. *Journal of Applied Ecology* **52**: 1425–1435.
- Martin AR, Rapidel B, Roupsard O, Van den Meersche K, de Melo Virginio Filho E, Barrios M, Isaac ME. 2017.** Intraspecific trait variation across multiple scales: the leaf economics spectrum in coffee. *Functional Ecology* **31**: 604–612.
- McClellan PE, Burrridge J, Beebe S, Rao IM, Porch TG. 2011.** Crop improvement in the era of climate change: an integrated, multi-disciplinary approach for common bean (*Phaseolus vulgaris*). *Functional Plant Biology* **38**: 927.
- McCormack ML, Kaproth MA, Cavender-Bares J, Carlson E, Hipp AL, Han Y, Kennedy PG. 2020.** Climate and phylogenetic history structure morphological and architectural trait variation among fine-root orders. *New Phytologist* **228**: 1824–1834.
- Messier J, McGill BJ, Enquist BJ, Lechowicz MJ. 2017.** Trait variation and integration across scales: is the leaf economic spectrum present at local scales? *Ecography* **40**: 685–697.
- Milla R, Morente-López J, Alonso-Rodrigo JM, Martín-Robles N, Stuart Chapin F. 2014.** Shifts and disruptions in resource-use trait syndromes during the evolution of herbaceous crops. *Proceedings of the Royal Society B: Biological Sciences* **281**: 20141429.
- Milla, Osborne CP, Turcotte MM, Violle C. 2015.** Plant domestication through an ecological lens. *Trends in Ecology & Evolution* **30**: 463–469.
- Milla R, Matesanz S. 2017.** Growing larger with domestication: a matter of physiology, morphology or allocation? *Plant Biology* **19**: 475–483.
- Moeiniazade S, Kusmec A, Hu G, Wang L, Schnable PS. 2020.** Multi-trait Genomic Selection Methods for Crop Improvement. *Genetics* **215**: 931–945.
- Montazeaud G, Violle C, Fréville H, Luquet D, Ahmadi N, Courtois B, Bouhaba I, Fort F. 2018.** Crop mixtures: does niche complementarity hold for belowground resources? An experimental test using rice genotypic pairs. *Plant and Soil* **424**: 187–202.
- Montazeaud G, Rousset F, Fort F, Violle C, Fréville H, Gandon S. 2020a.** Farming plant cooperation in crops. *Proceedings of the Royal Society B: Biological Sciences* **287**: 20191290.

- Montazeaud G, Violle C, Roumet P, Rocher A, Ecartot M, Compan F, Maillet G, Fort F, Fréville H. 2020b.** Multifaceted functional diversity for multifaceted crop yield: Towards ecological assembly rules for varietal mixtures. *Journal of Applied Ecology* **57**: 2285–2295.
- Mouillot D, Loiseau N, Grenié M, Algar AC, Allegra M, Cadotte MW, Casajus N, Denelle P, Guéguen M, Maire A, et al. 2021.** The dimensionality and structure of species trait spaces. *Ecology Letters* **24**: 1988–2009.
- Niinemets Ü. 2015.** Is there a species spectrum within the world-wide leaf economics spectrum? Major variations in leaf functional traits in the Mediterranean sclerophyll *Quercus ilex*. *New Phytologist* **205**: 79–96.
- Peleg Z, Fahima T, Korol AB, Abbo S, Saranga Y. 2011.** Genetic analysis of wheat domestication and evolution under domestication. *Journal of Experimental Botany* **62**: 5051–5061.
- Peng JH, Sun D, Nevo E. 2011.** Domestication evolution, genetics and genomics in wheat. *Molecular Breeding* **28**: 281–301.
- Phillips PC, Arnold SJ. 1989.** Visualizing Multivariate Selection. *Evolution* **43**: 1209–1222.
- Pujol B, Salager J-L, Beltran M, Bousquet S, McKey D. 2008.** Photosynthesis and leaf structure in domesticated cassava (Euphorbiaceae) and a close wild relative: have leaf photosynthetic parameters evolved under domestication? *Biotropica* **40**: 305–312.
- R Core Team. 2022.** R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Reich PB. 2014.** The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**: 275–301.
- Richardson AE, Lynch JP, Ryan PR, Delhaize E, Smith FA, Smith SE, Harvey PR, Ryan MH, Veneklaas EJ, Lambers H, et al. 2011.** Plant and microbial strategies to improve the phosphorus efficiency of agriculture. *Plant and Soil* **349**: 121–156.
- Rimbert H, Darrier B, Navarro J, Kitt J, Choulet F, Leveugle M, Duarte J, Rivière N, Eversole K, Consortium on behalf of TIWGS, et al. 2018.** High throughput SNP discovery and genotyping in hexaploid wheat. *PLOS ONE* **13**: e0186329.
- Rolhauser AG, Windfeld E, Hanson S, Wittman H, Thoreau C, Lyon A, Isaac ME. 2022.** A trait–environment relationship approach to participatory plant breeding for organic agriculture. *The New Phytologist* **235**: 1018–1031.
- Rosielle AA, Frey KJ. 1975.** Estimates of selection parameters associated with harvest index in oat lines derived from a bulk population. *Euphytica* **24**: 121–131.
- Roucou A, Violle C, Fort F, Roumet P, Ecartot M, Vile D. 2018.** Shifts in plant functional strategies over the course of wheat domestication. *Journal of Applied Ecology* **55**: 25–37.
- Salguero-Gómez R, Violle C, Gimenez O, Childs D. 2018.** Delivering the promises of trait-based approaches to the needs of demographic approaches, and vice versa. *Functional Ecology* **32**: 1424–1435.

- Sartori K, Vasseur F, Violle C, Baron E, Gerard M, Rowe N, Ayala-Garay O, Christophe A, Jalón LG de, Masclef D, et al. 2019.** Leaf economics and slow-fast adaptation across the geographic range of *Arabidopsis thaliana*. *Scientific Reports* **9**: 10758.
- Segrestin J, Bernard-Verdier M, Violle C, Richarte J, Navas M-L, Garnier E. 2018.** When is the best time to flower and disperse? A comparative analysis of plant reproductive phenology in the Mediterranean. *Functional Ecology* **32**: 1770–1783.
- Shipley B, De Bello F, Cornelissen JHC, Laliberté E, Laughlin DC, Reich PB. 2016.** Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia* **180**: 923–931.
- Shoval O, Sheftel H, Shinar G, Hart Y, Ramote O, Mayo A, Dekel E, Kavanagh K, Alon U. 2012.** Evolutionary Trade-Offs, Pareto Optimality, and the Geometry of Phenotype Space. *Science* **336**: 1157–1160.
- Sugiura N. 1978.** Further analysis of the data by Akaike's information criterion and the finite corrections. *Communications in Statistics - Theory and Methods* **7**: 13–26.
- Vasseur F, Violle C, Enquist BJ, Granier C, Vile D. 2012.** A common genetic basis to the origin of the leaf economics spectrum and metabolic scaling allometry. *Ecology Letters* **15**: 1149–1157.
- Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007.** Let the concept of trait be functional! *Oikos* **116**: 882–892.
- Wainwright PC, Alfaro ME, Bolnick DI, Hulsey CD. 2005.** Many-to-One Mapping of Form to Function: A General Principle in Organismal Design?1. *Integrative and Comparative Biology* **45**: 256–262.
- Walker AP, McCormack ML, Messier J, Myers-Smith IH, Wulschleger SD. 2017.** Trait covariance: the functional warp of plant diversity? *The New Phytologist* **216**: 976–980.
- Watt M, Kirkegaard JA, Passioura JB, Watt M, Kirkegaard JA, Passioura JB. 2006.** Rhizosphere biology and crop productivity—a review. *Soil Research* **44**: 299–317.
- Weemstra M, Mommer L, Visser EJW, Ruijven J van, Kuyper TW, Mohren GMJ, Sterck FJ. 2016.** Towards a multidimensional root trait framework: a tree root review. *New Phytologist* **211**: 1159–1169.
- Weemstra M, Freschet GT, Stokes A, Roumet C. 2021.** Patterns in intraspecific variation in root traits are species-specific along an elevation gradient (E Sayer, Ed.). *Functional Ecology* **35**: 342–356.
- Weigelt A, Mommer L, Andrzejek K, Iversen CM, Bergmann J, Bruelheide H, Fan Y, Freschet GT, Guerrero-Ramírez NR, Kattge J, et al. 2021.** An integrated framework of plant form and function: the belowground perspective. *New Phytologist* **232**: 42–59.
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002.** Plant Ecological Strategies: Some Leading Dimensions of Variation Between Species. *Annual Review of Ecology and Systematics* **33**: 125–159.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, et al. 2004.** The worldwide leaf economics spectrum. *Nature* **428**: 821–827.
- Xie Q, Mayes S, Sparkes DL. 2016.** Optimizing tiller production and survival for grain yield improvement in a bread wheat × spelt mapping population. *Annals of Botany* **117**: 51–66.

Yang J, Cao M, Swenson NG. 2018. Why Functional Traits Do Not Predict Tree Demographic Rates. *Trends in Ecology & Evolution* **33**: 326–336.

York LM, Nord E, Lynch J. 2013. Integration of root phenes for soil resource acquisition. *Frontiers in Plant Science* **4**.

Yuan W, Peng S, Cao C, Virk P, Xing D, Zhang Y, Visperas RM, Laza RC. 2011. Agronomic performance of rice breeding lines selected based on plant traits or grain yield. *Field Crops Research* **121**: 168–174.

SUPPLEMENTARY INFORMATION

Plant trait relationships are maintained within a major crop species: lack of artificial selection signal and potential for improved agronomic performance

XII. Supporting Information

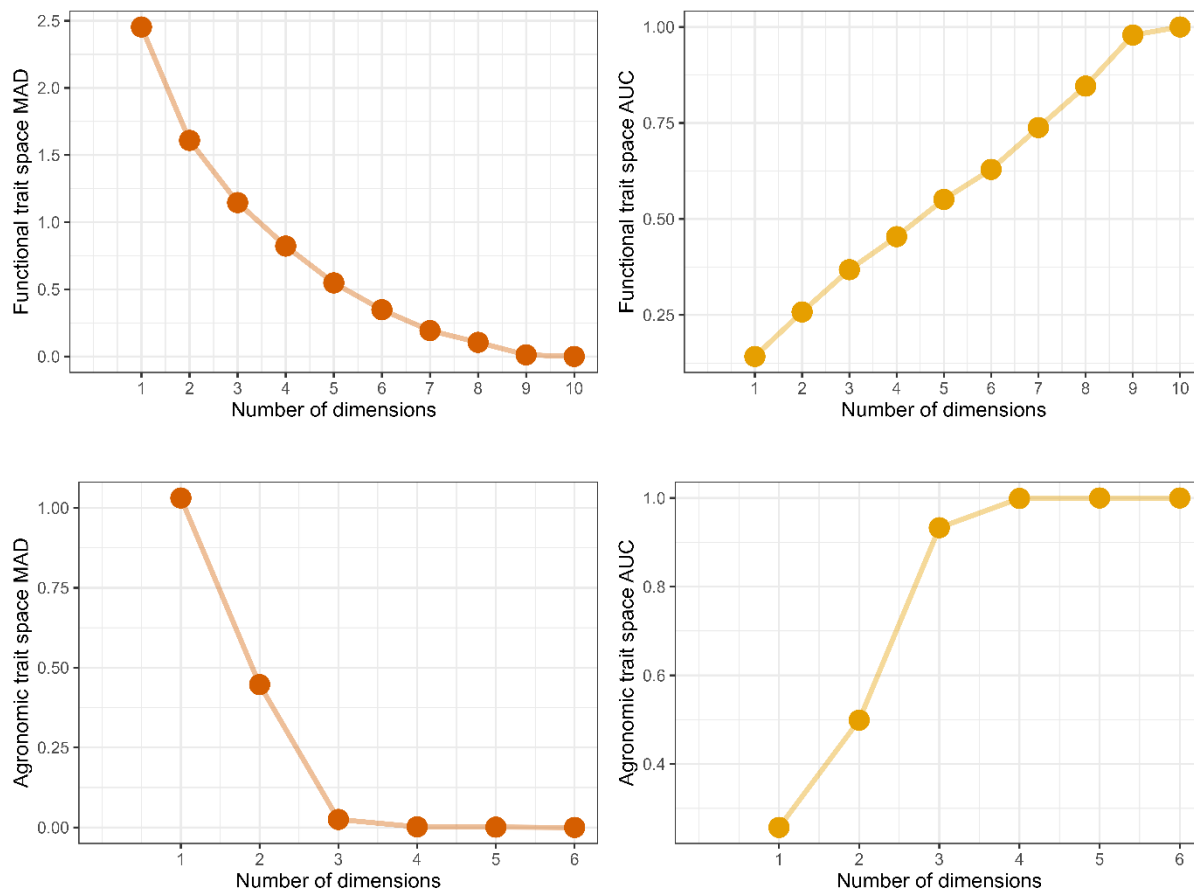


Fig. S1 Influence of the number of dimensions (number of retained PCA axes) used to build functional trait and agronomic trait spaces, on the space quality assessed by the area under the curve (AUC) criteria and the mean absolute deviation (MAD). The elbow method aims at maximising a given benefit (AUC gain) while reducing the cost (number of dimensions). Gain for the MAD is marginal after 4 dimensions for the functional trait space and three dimensions for the agronomic trait space.

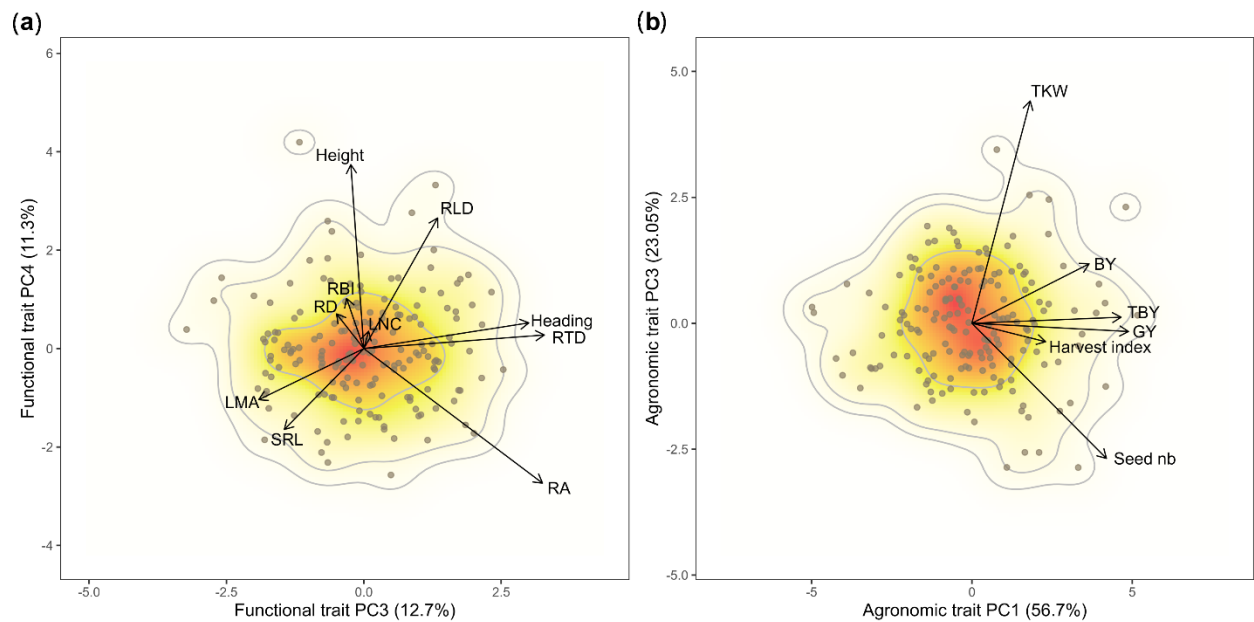


Fig. S2 (a) Representation of the structure of the above- and belowground functional space of the 179 durum wheat lines (*Triticum turgidum* spp. *durum*) according to the last two components of the principal component analysis. (A) above- and belowground functional traits: Heading (degree days): Heading date; Height (cm): maximal plant height, LMA (kg m^{-2}): Leaf mass area; LNC (%): Leaf nitrogen content; RA ($^{\circ}$): Root angle; RBI (number of tips per length unit): Root branching intensity; RD (mm): Root diameter; RLD (cm cm^{-3}): Root length density; RTD (g cm^{-3}): Root tissue density and SRL (m g^{-1}): Specific root length; (b) Structure of the agronomic trait space of the 179 durum wheat genotypes according to the first and the third components of the principal component analysis. The agronomic traits illustrate productivity at the vegetative and/or reproductive stages. BY (g m^{-2}): Biomass yield; GY (g m^{-2}): Grain yield; Harvest index: Harvest index; Seed nb: Seed number per m^2 ; TBY (g m^{-2}): Total biomass yield; TKW (g): Thousand kernel weight. The colour gradient and contour lines correspond to the 0.5, 0.95 and 0.99 quantiles of the respective probability distribution, thus highlighting the regions of highest and lowest trait occurrence probability.

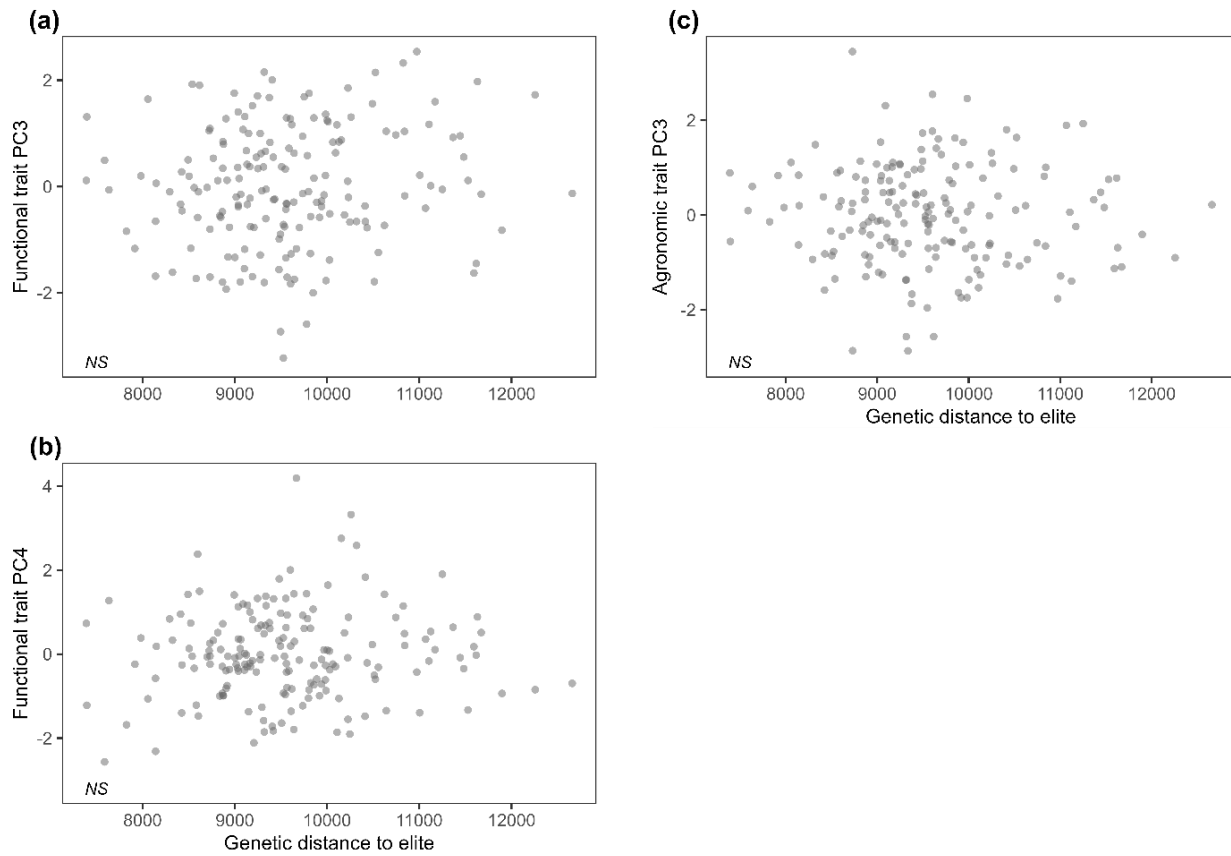


Fig. S3 Relationships between the genetic distance to the elite compartment (*Triticum turgidum* *ssp. durum*) and the last components of the functional trait space ((a): PC3, (b): PC4) and the agronomic trait space (c): PC3). For each relationship, the adjusted coefficient of determination R^2 is given. Significance: *NS*, not significant; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

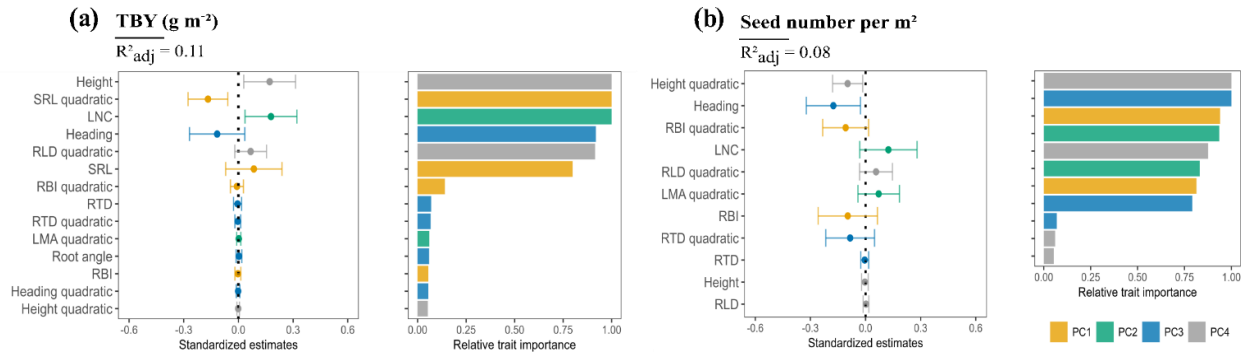


Fig. S4 Standardized effects of functional traits on agronomic traits including total biomass yield (TBY, g m^{-2} , (a)) and seed number per m^2 (b). Above- and belowground functional traits: Heading date in degree days (Heading); Maximal plant height in cm (Height); Leaf mass area in kg m^{-2} (LMA); Leaf nitrogen content in % (LNC); Root angle ($^{\circ}$); Root branching intensity in number of tips per length unit (RBI); Root length density in cm cm^{-3} (RLD); Root tissue density in g cm^{-3} (RTD): and Specific root length in m g^{-1} (SRL). A quadratic term was added in the models to test non-linear relationships between functional traits and agronomic traits. The relative importance of functional traits is reported on the right side of the four panels and can be interpreted as the probability that the trait is in the best model. The N best models based on an AICc difference lower than two were retained to compute model-averaged estimates reported on the left side of the two panels with their 95% unconditional confidence intervals. Colours refer to the dimensions of the functional trait space where the trait contributes most. Adjusted R-squared averaged across the N best models (R^2_{adj}) are also presented for the two models.

Table S1 Names of the eight elite wheat varieties (*Triticum turgidum* spp. *durum*) used to calculate the average genetic distances with the 179 genotypes proposed in the study and their date of registration in the catalog (<https://www.semae.fr/catalogue-varietes/>).

Varieties name	Registration date
Dakter	2005
Isildur	2007
Liberdur	2007
Pescadou	2001
Ixos	2004
Lloyd	2007
Neodur	1987
Primadur	2007

Table S2 Best fitting models between biomass yield (BY) and functional traits, which were used to compute model-averaged estimates reported in the main text (Fig. 3a). Above- and belowground functional traits: Heading date in degree days (Heading); Maximal plant height in cm (Height); Leaf mass area in kg m⁻² (LMA); Leaf nitrogen content in % (LNC); Root angle (°); Root branching intensity in number of tips per length unit (RBI); Root length density in cm cm⁻³ (RLD); Root tissue density in g cm⁻³ (RTD) and Specific root length in m g⁻¹ (SRL) The best N models are ranked according to their AICc. ΔAICc, model weights, and adjusted R-squared (R² adj) are reported for the models. Colours show which principal component of the functional space the trait contributes most to.

ΔAICc	Weights	R2-adjusted	Height	Height quadratic	Heading	Heading quadratic	LMA	LMA quadratic	LNC	SRL	SRL quadratic	RLD	RLD quadratic	Root angle	Root angle quadratic	RBI	RTD
0.000	0.105	0.315	█						█		█						█
0.056	0.102	0.310	█						█		█						█
1.462	0.051	0.314							█		█					█	█
1.570	0.048	0.313							█		█					█	█
1.575	0.048	0.313		█					█		█						█
1.705	0.045	0.313							█		█						█
1.734	0.044	0.313							█		█						█
1.779	0.043	0.308							█		█						█
1.779	0.043	0.312							█		█						█
1.870	0.041	0.312							█		█						█
1.871	0.041	0.312							█		█						█
1.895	0.041	0.308							█		█						█
1.912	0.041	0.307							█		█						█
1.957	0.040	0.312							█		█						█

Table S3 Best fitting models between grain yield (GY) and functional traits, which were used to compute model-averaged estimates reported in the main text (Fig. 3b). Above- and belowground functional traits: Heading date in degree days (Heading); Maximal plant height in cm (Height); Leaf mass area in kg m⁻² (LMA); Leaf nitrogen content in % (LNC); Root angle (°); Root branching intensity in number of tips per length unit (RBI); Root diameter in mm (RD); Root length density in cm cm⁻³ (RLD); Root tissue density in g cm⁻³ (RTD). The best N models are ranked according to their AICc. ΔAICc, model weights, and adjusted R-squared (R² adj) are reported for the models. Colours show which principal component of the functional space the trait contributes most to.

ΔAICc	Weights	R2-adjusted	Height	Height quadratic	Heading	LMA	LMA quadratic	LNC	RD	RD quadratic	RLD	RLD quadratic	RBI	RBI quadratic	RTD
0.000	0.099	0.156			■		■		■					■	■
0.134	0.093	0.161			■		■		■					■	■
0.885	0.064	0.146			■		■		■	■				■	■
1.244	0.053	0.145			■		■		■					■	■
1.408	0.049	0.155			■		■		■					■	■
1.423	0.049	0.155		■	■		■		■		■			■	■
1.702	0.042	0.154	■		■		■		■					■	■
1.839	0.040	0.153			■		■		■				■	■	■
1.897	0.038	0.153			■		■		■				■	■	■

Table S4 Best fitting models between harvest index and functional traits, which were used to compute model-averaged estimates reported in the main text (Fig. 3c). Above- and belowground functional traits: Heading date in degree days (Heading); Maximal plant height in cm (Height); Leaf mass area in kg m⁻² (LMA); Leaf nitrogen content in % (LNC); Root angle (°); Root branching intensity in number of tips per length unit (RBI); Root diameter in mm (RD); Root length density in cm cm⁻³ (RLD); Root tissue density in g cm⁻³ (RTD). The best N models are ranked according to their AICc. ΔAICc, model weights, and adjusted R-squared (R² adj) are reported for the models. Colours show which principal component of the functional space the trait contributes most to.

ΔAICc	Weights	R2-adjusted	Height	Height quadratic	Heading	Heading quadratic	LMA	LMA quadratic	LNC quadratic	RD	RLD	RLD quadratic	RBI	RBI quadratic	Root angle	RTD
0.000	0.090	0.248														
0.302	0.077	0.252														
0.368	0.075	0.252														
0.845	0.059	0.250														
0.934	0.056	0.240														
1.034	0.054	0.239														
1.106	0.052	0.249														
1.140	0.051	0.249														
1.283	0.047	0.248														
1.668	0.039	0.252														
1.753	0.037	0.246														
1.844	0.036	0.236														

Table S5 Best fitting models between thousand kernel weight and functional traits, which were used to compute model-averaged estimates reported in the main text (Fig. 3d). Above- and belowground functional traits: Heading date in degree days (Heading); Maximal plant height in cm (Height); Leaf mass area in kg m^{-2} (LMA); Leaf nitrogen content in % (LNC); Root angle ($^{\circ}$); Root branching intensity in number of tips per length unit (RBI); Root diameter in mm (RD); Root length density in cm cm^{-3} (RLD); Root tissue density in g cm^{-3} (RTD). The best N models are ranked according to their AICc. ΔAICc , model weights, and adjusted R-squared (R^2 adj) are reported for the models. Colours show which principal component of the functional space the trait contributes most to.

ΔAICc	Weights	R2-adjusted	Height	Heading	LMA	LMA quadratic	LNC	LNC quadratic	RD	RLD	RLD quadratic	RBI	RBI quadratic	Root angle	Root angle quadratic	RTD	RTD quadratic
0.000	0.057	0.220															
0.051	0.056	0.225															
0.128	0.054	0.214															
0.281	0.050	0.224															
0.537	0.044	0.228															
0.543	0.044	0.222															
0.645	0.042	0.217															
0.833	0.038	0.216															
0.895	0.037	0.226															
1.076	0.034	0.220															
1.207	0.031	0.230															
1.253	0.031	0.225															
1.254	0.031	0.219															
1.336	0.029	0.224															
1.698	0.025	0.217															
1.901	0.022	0.227															
1.911	0.022	0.217															
1.914	0.022	0.222															
1.982	0.021	0.216															
1.996	0.021	0.216															

Table S6 Correlation coefficients between traits and PC axes for the functional trait space and the agronomic trait space, each built with the 179 durum wheat lines. LNC, Leaf nitrogen content (%); LMA, Leaf mass area (kg m^{-2}); Height, maximal plant height (cm); RD, Root diameter (mm); SRL, Specific root length (m g^{-1}); RTD, Root tissue density (g cm^{-3}); RBI, Root branching intensity (number of tips per length unit); RLD, Root length density (cm cm^{-3}); Heading, Heading date (degree days); RA, Root angle ($^{\circ}$); GY, Grain yield (g m^{-2}); BY, Biomass yield (g m^{-2}); TBY, Total biomass yield (g m^{-2}); TKW, Thousand kernel weight (g); Seed number, Seed number per m^2 ; Harvest index, Harvest index.

Functional trait space					Agronomic trait space			
<i>Traits</i>	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>	<i>PC4</i>	<i>Traits</i>	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>
LNC	0.29	0.73	0.02	0.06	GY	0.98	0.20	-0.03
LMA	-0.06	-0.69	0.35	-0.19	BY	0.73	-0.61	0.24
Height	-0.25	0.19	-0.04	0.68	TBY	0.93	-0.34	0.02
RD	0.91	-0.07	-0.09	0.13	TKW	0.36	0.29	0.88
SRL	-0.73	0.48	-0.26	-0.30	Seed number	0.84	0.06	-0.53
RTD	-0.28	-0.51	0.6	0.05	Harvest index	0.46	0.88	-0.07
RBI	0.75	-0.12	-0.06	0.18				
RLD	-0.46	0.26	0.24	0.48				
Heading	0.08	0.39	0.55	0.09				
RA	0.22	0.04	0.59	-0.5				



Première forme domestiquée de blé dur

A. Rimlinger

CHAPITRE 2

*Domesticated plants performed better under competition
than their wild progenitors despite lower phenotypic
plasticity*

Article en préparation

Lemoine, T., Violle, C., Gonzalez, E. A., Gaubert, M., Rocher, A., Fréville, H., & Fort, F. (2023). Domesticated plants performed better under competition than their wild progenitors despite lower phenotypic plasticity. *In Prep.*

I. Présentation générale

Les environnements des cultures (perturbé, fertile, compétitif) ont probablement amené les espèces cultivées à s'adapter à la compétition (Milla, 2023). La sélection dans ces environnements a favorisé des plantes avec une forte biomasse, une grande stature, des feuilles larges associées et de grosses graines (Milla *et al.*, 2014; Milla & Matesanz, 2017; Roucou *et al.*, 2018). Ce phénotype est caractéristique d'un phénotype compétiteur pour la lumière. **L'objectif de cette deuxième partie est d'examiner comment la réponse à la compétition varie au cours de la domestication et de la sélection moderne chez le blé dur.** Nous nous attendons à ce que les formes domestiquées soient plus performantes en réponse à la compétition que les formes sauvages du blé, du fait que les environnements des cultures ont probablement favorisé des valeurs de traits leur permettant de faire face à des environnements compétitifs.

Pour le tester, nous mesurons un panel de traits aériens et souterrains chez 39 génotypes, caractéristiques des stades clé de la domestication et de l'amélioration variétale chez le blé dur. Pour évaluer la réponse à la compétition, nous plaçons les différents génotypes en compétition avec un même concurrent voisin cultivé à une densité plus élevée (Goldberg & Fleetwood, 1987; Goldberg & Werner, 1983). Les génotypes sont donc semés soit seul dans un pot soit en compétition avec quatre voisins identiques. Ce voisin est un génotype élite différent des 39 autres génotypes, prédisposé pour être un bon concurrent en raison de sa grande stature. Afin d'explorer comment le phénotype du blé dur a varié au cours de sa domestication, nous analysons dans un premier temps les différences de valeurs de traits entre chaque compartiment du blé dur. Nous estimons ensuite la réponse à la compétition des traits de performance (biomasse totale, biomasse végétative...) et des traits fonctionnels (hauteur, surface foliaire...) en utilisant l'indice de réponse à la compétition (R_m) (Keddy *et al.*, 1998; Navas & Garnier, 2002), permettant d'évaluer à la fois la direction et l'amplitude de la réponse. Nous utilisons l'indice estimé à partir de la biomasse totale comme indicateur de la performance de la plante en réponse à la compétition. Plus cet indice est proche de zéro moins la plante a perdu de biomasse en réponse à la compétition. Nous comparons la réponse des traits fonctionnels et de performance à la compétition (R_m) entre les différents compartiments du blé. Dans un second temps, nous cherchons à savoir ce qui explique le mieux la

réponse à la compétition : les valeurs des traits fonctionnels en conditions isolés, les valeurs des traits fonctionnels en compétition ou la plasticité des traits en réponse à la compétition. Pour cela, nous testons les relations entre la réponse à la compétition (indice basé sur la biomasse totale) et ces trois composantes. Dans ce chapitre, nous montrons que les formes domestiquées sont plus performantes en réponse à la compétition que les génotypes sauvages du blé. Nous mettons en évidence que la plasticité de certains traits en réponse à la compétition est plus importante dans le compartiment sauvage. Enfin, nous trouvons que les traits en compétition et la plasticité phénotypique explique une part importante de la réponse à la compétition des génotypes.

II. Abstract

- Increasing yield by reducing competition among plants within fields has been a landmark step in plant domestication. However, we know little about the effects of domestication and breeding on the competitive response of crops, *i.e.* the ability of plants to tolerate a decrease in resource availability due to competition. Domestication and the highly competitive environments of cropping systems probably led to the adaptation of cereals to competition. Moreover, directional selection also normalized the phenotype of crops, with modern breeding selecting toward varieties suited for wide environments and thus likely with reduced phenotypic plasticity. We thus expect crops to have evolved towards reduced ability to respond to neighbours. Yet, this hypothesis remains poorly explored experimentally. Here, we investigated whether crop domestication and breeding have modulated plant competitive response.
- We used a collection of 39 genotypes representative of the four key stages (wild, first domesticated, landrace and elite) in the evolutionary history of durum wheat, from wild progenitors to elite lines. We grew them in pots in a common garden experiment, alone and with the same competitive genotype, and measured above- and belowground functional traits and performance traits to assess competitive response.
- We highlighted significant differences in competitive response among the four compartments, highlighting that the direction of intentional or unintentional selection varied over the course of domestication. Interestingly, we found that the three domesticated compartments lost less total biomass in response to competition than wild progenitors, highlighting that domestication promoted the ability of crops to cope with competition.
- In response to competition, all compartments invested in thinner leaves and thickened their roots. Most functional traits were plastic in response to competition in all compartments, but plasticity was significantly stronger in the wild compartment. Aboveground trait values under competition and phenotypic plasticity were major drivers of wheat performance under competition.

III. Keywords

Breeding, crop domestication, durum wheat, functional traits, plant competition, plasticity, response to competition.

IV. Introduction

Selecting for individuals who are weak competitors in order to improve crop grain yield has been a long-standing working hypothesis since the advent of modern breeding (Donald, 1963, 1968; Sadras *et al.*, 2011; Denison, 2015; Wuest *et al.*, 2021; Fréville *et al.*, 2022). It was supported by the conceptual thinking of the crop ideotype (Donald, 1968), and more recently by the theoretical corpus of the tragedy of the commons (Anten & Vermeulen, 2016; Weiner, 2019; Biernaskie, 2022). In these theoretical frameworks, individuals that are weak competitors, when they are grown together with individuals that share the same phenotype, maximise grain productivity of the group (e.g., Weiner, 2019; Montazeaud *et al.*, 2020). The introgression of semi-dwarfing genes in cereals during the Green Revolution to produce shorter plants resistant to lodging in high-input environments has led to spectacular yield improvement and is seen as one emblematic example supporting the "weak competitor ideotype" concept (Donald, 1968; Weiner, 2019; Biernaskie, 2022). Plant breeders have long sought to limit competitive interactions by decreasing the ability of plants to reduce the performance of their neighbours (namely, *competitive effect*). Surprisingly, competition within crops remains little explored from the standpoint of the plant ability to tolerate a decrease in resource availability due to the presence of a competitor (namely, *competitive response*; Goldberg & Fleetwood, 1987; Goldberg, 1990).

A major challenge associated to the evaluation of competitive ability is to identify plant traits that can predict it, as investigated across myriad of wild species in plant ecology (Fargione & Tilman, 2006; Cahill & Lamb, 2007; Funk & Wolf, 2016; Kunstler *et al.*, 2016). Plant comparative ecology has made major progress in the quantification of the link between plant traits and their competitive ability thanks to ambitious screening programs (Grime & Hunt, 1975; Grime, 1977; Keddy & Shipley, 1989; Kunstler *et al.*, 2016). This work was rooted on the assumption that plant functional traits measured under optimal conditions for a set of species can predict their performance in response to environmental drivers, i.e. their strategy (Keddy, 1992). One

emblematic example is the classification of plant species along a “C” (competition) axis, based on the set of trait values expected to related to competitive ability (Grime, 1977). This idea comes together with the functional trait-to performance mapping proposed in functional ecology (Violle *et al.*, 2007): functional traits measured on organ- or whole-plant scales interplay to explain variation in traits more tightly linked to plant fitness, named performance traits (e.g., seed number, plant biomass). Although trait values in response to competition have been presented as relevant indicators to explain plant performance under competition (Violle *et al.*, 2009), it remains unclear whether traits measured on plants grown alone, traits measured on plants grown in competition or phenotypic plasticity in response to competition best predict plant performance under competition.

Plants can express phenotypic plasticity and thus adjust their trait values in response to the presence of neighbours. For example, specific leaf area, which is strongly influenced by light levels, increases in response to light depletion caused by competitors (Valladares *et al.*, 2000; Violle *et al.*, 2009). Root anatomy and morphology, such as root branching or elongation rate, are also sensitive to changing soil nutrient and water availabilities in response to plant competition (Schenk, 2006). These changes might be associated to the ability of plants to: (i) tolerate competition and acquire resources under shade or nutrient stress conditions, (ii) escape competition spatially or temporally, and (iii) confront to competitors through, for example, competition-induced allelopathy (Novoplansky, 2009). Plasticity can thus confer greater competitive ability, for example, through greater development of organs responsible for resource acquisition (e.g., Crick & Grime, 1987; Bret-Harte *et al.*, 2001). Despite the huge number of experimental and modelling studies on plasticity to competition (e.g., Sorrensen-Cothorn *et al.*, 1993; Callaway *et al.*, 2003; Grams & Andersen, 2007; Valladares *et al.*, 2007; Fort *et al.*, 2014), there is still no consensus on the role of phenotypic plasticity in driving the outcome of plant-plant interactions. In addition, although it has been suggested that phenotypic plasticity has been counter-selected over the course of domestication and breeding (Kebrom & Brutnell, 2007), this hypothesis remains to be investigated.

Crop species represent a unique opportunity to test changes in competitive response following intentional or unintentional human selection, and to identify its phenotypic drivers. Domestication, breeding and agricultural practices have induced changes in plant morphology (Gioia *et al.*, 2015; Roucou *et al.*, 2018; Spor *et al.*, 2020; Isaac *et al.*, 2021), physiology (Meyer *et al.*, 2012; Turcotte *et al.*, 2014; Welcker *et al.*, 2022), reproduction (Purugganan & Fuller, 2009;

Fuller *et al.*, 2014) and dispersal (Harlan *et al.*, 1973; Tanno & Willcox, 2012), gradually distancing phenotypically and genetically cultivated species from their wild progenitors. Thus, domesticated herbaceous crops tend to express aboveground phenotypes with an erect architecture composed of a small number of tillers, associated with highly resource-acquiring leaf traits and a higher biomass compared to their wild progenitors (Milla *et al.*, 2014; Chen *et al.*, 2015; Milla & Matesanz, 2017; Roucou *et al.*, 2018; Martín-Robles *et al.*, 2019). For the underground compartment, recent evidence also suggests a shift in root traits towards a more resource acquisition strategy over the course of plant domestication (Roucou *et al.*, 2018) even if the response differed between species (Martín-Robles *et al.*, 2019). All these reported phenotypic changes suggest selection towards greater competitive ability for the most domesticated plants, but a direct evaluation is still surprisingly lacking.

Using 39 genotypes clustered into four genetic compartments representative of durum wheat domestication and breeding (Roucou *et al.*, 2018), we tested whether: i) functional and performance traits values differ among genetic compartments; ii) the response of functional and performance traits to competition varies between compartments; iii) which of functional trait values measured on plants grown alone, plants grown in competition and phenotypic plasticity in response to competition best explains performance traits under competition. We hypothesized that domesticated forms would better tolerate competition than their wild progenitors, given the selective pressures of domestication, breeding and agricultural practices on cereals, which likely modulated the trait values of the domesticated forms to enable them to better tolerate competitive environments. In addition, we expected wild progenitors to be more plastic to competition than elite genotypes given the strong constraints exerted by artificial selection to produce stable varieties in a wide range of environments. Disentangling competitive effect and competitive response can be very complex since a given plant is simultaneously impacted by resource depletion by neighbours (*competitive response*) but also removes part of resources available for these neighbours (*competitive effect*) (Goldberg & Fleetwood, 1987; Goldberg & Landa, 1991; Keddy *et al.*, 1998; Foster, 2000; Violle *et al.*, 2009). Experimental designs have been thoroughly thought to specifically assess the response of a given focal plant to competition while minimizing the competitive effect it can have on its competitors (Goldberg & Fleetwood, 1987; Goldberg & Werner, 1983). In short, the idea is to compare the performance of different focal species (or genotypes) in response to the same neighbouring competitor grown at higher density (Fig. 1). This

standardized design allows to accurately assess the competitive response of plants through a comparative approach (Goldberg & Werner, 1983), provided that the neighbour is selected based on its strong competitive effect (e.g., tall plants). Here, we proposed for the time to apply such an experimental framework to evaluate the changes in competitive response over the course of plant domestication.

V. Material and methods

Plant material

We selected 39 accessions from the domestication and breeding history of the tetraploid wheat: 10 wild emmer accessions of the wild progenitor *T. turgidum* ssp. *dicoccoides* (W), 10 accessions of the first domesticated emmer *T. turgidum* ssp. *dicoccum* (FD), 10 landrace accessions of durum wheat *T. turgidum* ssp. *durum* belonging to the pre-Green Revolution period (DL), and 9 elite accessions of durum wheat registered in Europe after the Green Revolution (DE). Seeds were originally gathered from different international seed collections (Table S1). To ensure genetic homogeneity of seeds within accessions, accessions were further reproduced by successive self-fertilizations in common gardens by INRAE UMR AGAP, Montpellier, France.

Experimental design

We set up the experiment under outdoor conditions from January to May 2022 (minimal temperature = -3.3°C and maximal temperature = 28.6°C) in the experimental field of the “Centre d’Ecologie Fonctionnelle et Evolutive”, Montpellier, France (43° 63 ‘87’’N, 3° 86’ 26’’E). We performed a randomized complete block design using four blocks. The 39 genotypes were grown both alone, i.e., one individual per pot, and in competition with four individuals of another genotype (Fig. 1). This neighbour genotype is a durum wheat genotype different from the 39 selected as focal plants, which we expected to be a good competitor based on its ability to maintain a tall stature from early in the life-cycle to its maturity (Fig. S1). This genotype was also grown alone in order to measure its traits without competition. This resulted in a total of 324 pots (4-L, 18.5 cm diameter; 21.5 cm depth) in the experiment.

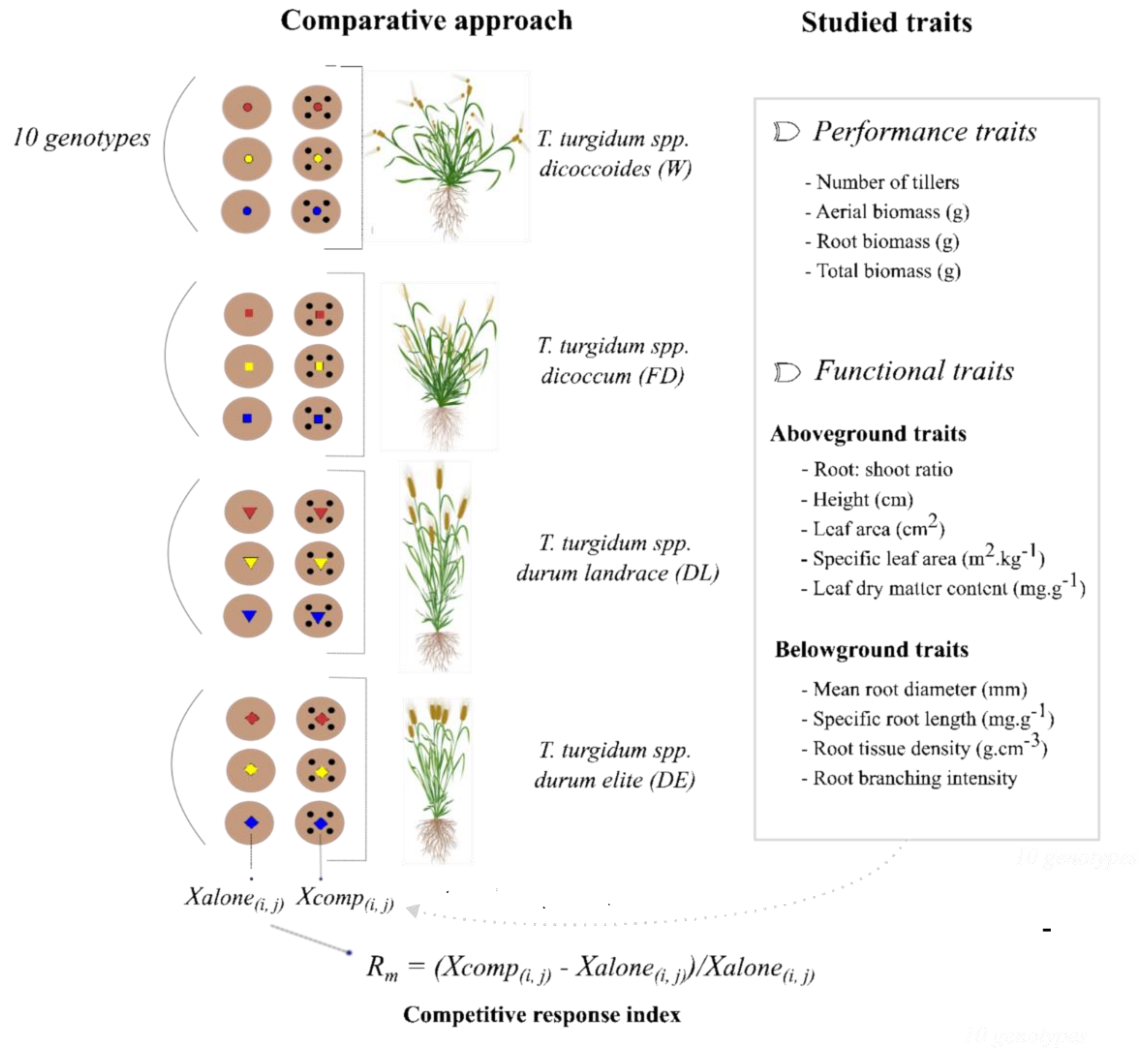


Figure 1. Experimental design to assess the response to competition over the course of wheat domestication and breeding using four domestication compartments from wild forms to elite genotypes. Neighbouring plants belong to a unique genotype used for all pots (black points; four plants per pot). Each focal genotype was grown alone and under competition. For each trait, phenotypic change in response to competition was estimated using the competitive response index (R_m).

Pots were placed on a tarpaulin on the ground and were interspaced (~30 cm) to avoid inter-pot competition for light. For each accession, two seeds were sown at the centre of each pot in order to face potential problems of seed germination. For the modality grown with a neighbour, eight of the neighbour's seeds (divided into four batches of two) were added to the pot (Fig. 1). Then the seedlings were thinned at the first leaf stage to obtain one plant per position. We used local soil from the experimental field, composed of a sandy clay-limestone (132 g/kg of sand (0.05 to 0.2

mm), 120 g/kg of silt (0.002 to 0.02) and 179 g/kg of clay; 75 g/kg of CaCO₃; 37.9 g/kg of organic carbon; 1.83 g/kg of total N; 0.0787 g/kg of P; pH 7.8). We fertilized plants with PK fertilizer (0.32 g per pot in total; P₂O₅ and K₂O) and ammonium nitrate (0.67 g per pot in total). Pots were watered with tap water two to three times a week depending on rainfall to avoid water excess and deficit. At the first appearance of *Septoria tritici* blotch and aphids, pots were treated, respectively, with Bordeaux mixture (mixture of copper(II) sulphate (CuSO₄) and quicklime (CaO)) and rapeseed oil.

Trait measurements

Functional and performance traits (Fig. 1) were measured at the beginning of ear emergence (after 110 days of growth). We measured aboveground traits for each focal genotype grown alone and in the competitive treatment, and for one neighbouring plant per pot from the competition treatment. First, we counted the number of tillers and measured plant height (cm). Then, we collected the second youngest leaf preceding the flag leaf on the longest tiller. Leaves showing symptoms of disease and herbivory were avoided. Leaves were stored 24h at 4°C in demineralized water to allow their rehydration (Pérez-Harguindeguy *et al.*, 2013). They were then weighed to obtain leaf fresh weight (g) and scanned (400 dpi). Leaf area (LA, cm²) was obtained using WinFolia software (Regent Instruments, Quebec, Canada). Leaves were then dried at 60°C for at least 72 hours and weighed to determine leaf dry weight (g). Specific leaf area (SLA, m².kg⁻¹) was calculated as the ratio of leaf area and leaf dry weight, and leaf dry matter content (LDMC, mg.g⁻¹) as the ratio of leaf dry weight and leaf fresh weight.

Afterward, we harvested separately the aboveground biomass of the plants grown alone, and of both the focal and neighbour plants in the competition treatment. Aboveground biomasses (Aerial biomass, g) were dried at least 72h at 60°C and weighted. Root systems were unpotted and washed. Then, the root systems of plants grown alone were immediately stored at -18°C, while the root systems of the focal plants grown under competition were carefully separated from those of their neighbours. Only the root system of the focal plant was kept for further analysis and stored at -18°C. After the harvest, root systems were defrosted, carefully washed and three to five adventitious roots of medium age were sampled. These subsamples were scanned at a resolution of 800 dpi (EPSON EXPRESSION 1680) to estimate the number of root tips, the distribution of root lengths among diameter classes, and total root length and volume using WinRHIZO (pro Version 2019; Regent Instrument). Mean root diameter (RD, mm) was calculated as the average of

the median root diameters of each diameter class weighted by the root length of each class. Specific root length (SRL, m.g^{-1}) was calculated as the ratio of the total length of the sample divided by its dry mass. We estimated root tissue density (RTD, g.cm^{-3}) as the ratio between dry mass and root volume of the subsample, and root branching intensity (RBI) as the ratio of the number of root tips of the subsample divided by its length. Root subsamples and the remaining roots of each focal plant were dried at least 72h at 60°C and weighted (Root biomass, g). We computed the total biomass of each focal plant by summing above- and belowground biomass (Total biomass, g).

Estimation of C score

We estimated for each genotype the competitive score (C) within the CSR triangle (Grime, 1977), based on leaf traits measurements, such as leaf area, specific leaf area and leaf dry matter content using the method developed by Pierce *et al.*, (2017). The leaf traits used in Pierce's method are leaf traits representative of the main axes of phenotypic variation in plants, i.e. the size variation axis and the resource acquisition-conservation axis (Reich, 2014; Díaz *et al.*, 2016). The competitive score was estimated for both focal leaf traits in isolated conditions and under competition.

Quantification of competitive response

For each focal genotype, we estimated changes in functional and performance trait values in response to competition, using the competitive response index (R_m ; Fig. 1) (Keddy *et al.*, 1998; Navas & Garnier, 2002), which allows evaluating both the magnitude and the direction of the response:

$$R_m = (X_{comp(i,j)} - X_{alone(i,j)}) / X_{alone(i,j)} \quad (\text{Eqn 1})$$

where $X_{comp(i,j)}$ is the trait value of the focal plant of a given genotype i grown in competition in block j and $X_{alone(i,j)}$ is the trait value of the focal plant of genotype i grown alone in block j . Negative values of R_m indicate that the trait value of the genotype grown in competition is smaller than when grown alone. A high R_m value indicates a large trait value difference between the two treatments. R_m is thus a measure of phenotypic plasticity. We used R_m based on plant total biomass as a proxy of plant performance in response to competition; the closer to zero, the less biomass loss in response to competition.

Data analyses

We first tested for differences in trait values among domestication compartments using the data coming only from pots where plants were grown alone. To do so, we used a linear mixed model (*lmer* function), where domestication compartments (wild, first domesticated, durum landrace, durum elite) were considered as a fixed effect, while block and genotype identity nested within domestication compartment were considered as random effects. We performed multiple comparison tests (Tukey method, *lsmeans* function and package) to test for differences between domestication compartments for each trait. Response variables were log transformed when necessary to meet normality assumptions.

To assess differences in trait values in response to the presence of neighbours along the domestication transect, we performed linear mixed models with domestication compartments, treatment (without vs with competition), and their interactions as fixed effects, and block and genotype identity nested within domestication compartment as random effects.

To further explore the effect of the interaction between domestication and treatment effects on trait values, we assessed differences in competitive response index (R_m), based on functional and performance traits, along the domestication transect, using a linear mixed model with domestication compartments as fixed effect (multiple comparison tests, Tukey method), block and genotype identity nested in domestication compartment as random effect. In addition, we tested whether R_m index was significantly different from 0 in each compartment, using a t-test.

For each functional trait, we tested whether competitive response R_m based on total biomass was better explained by the trait value in isolated conditions, in competition, or by phenotypic plasticity of the functional trait. To do so, we performed univariate linear mixed models, using as an explanatory variable: (i) focal trait values in pots without competition, then (ii) focal trait values in pots with competition, and lastly (iii) phenotypic plasticity expressed by the focal plant in response to competition (R_m of the functional trait), nested within domestication compartments as fixed effect or not (whole dataset), and block and genotype identity nested in domestication compartment as random effects.

We tested for C-scores differences between compartments and treatment, using the same linear mixed model as for testing differences in trait values in response to competition. Then, we tested

whether the competitive response R_m based on focal total biomass was explained by C-scores measured in isolated conditions, and in competition.

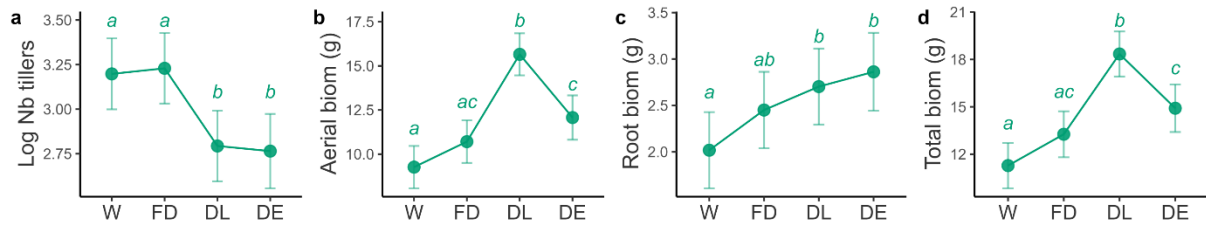
All statistical analyses were performed with R version 4.2.2 (R Core Team, 2022).

VI. Results

Trait variation over the course of wheat domestication and breeding in isolated conditions

Values of all four performance traits in isolated conditions significantly changed over the course of domestication and breeding (Fig. 2; Table 1A). Specifically, landraces and elite genotypes had a significantly lower number of tillers (respectively, $\mu = 17 \pm 2$, $\mu = 16 \pm 2$) than wild and first domesticated subspecies (respectively, $\mu = 26 \pm 2$, $\mu = 27 \pm 2$; Fig. 2a). Landraces and elite genotypes produced significantly more aerial biomass than wild genotypes (Fig. 2b). Root biomass increased over the course of domestication, with a significantly higher root biomass in landraces and elite genotypes compared to wild genotypes (Fig. 2c). Total biomass variation across compartments followed the same pattern as aerial biomass: landraces and elite genotypes produced significantly more total biomass than wild genotypes (Fig. 2d).

Performance traits



Functional traits

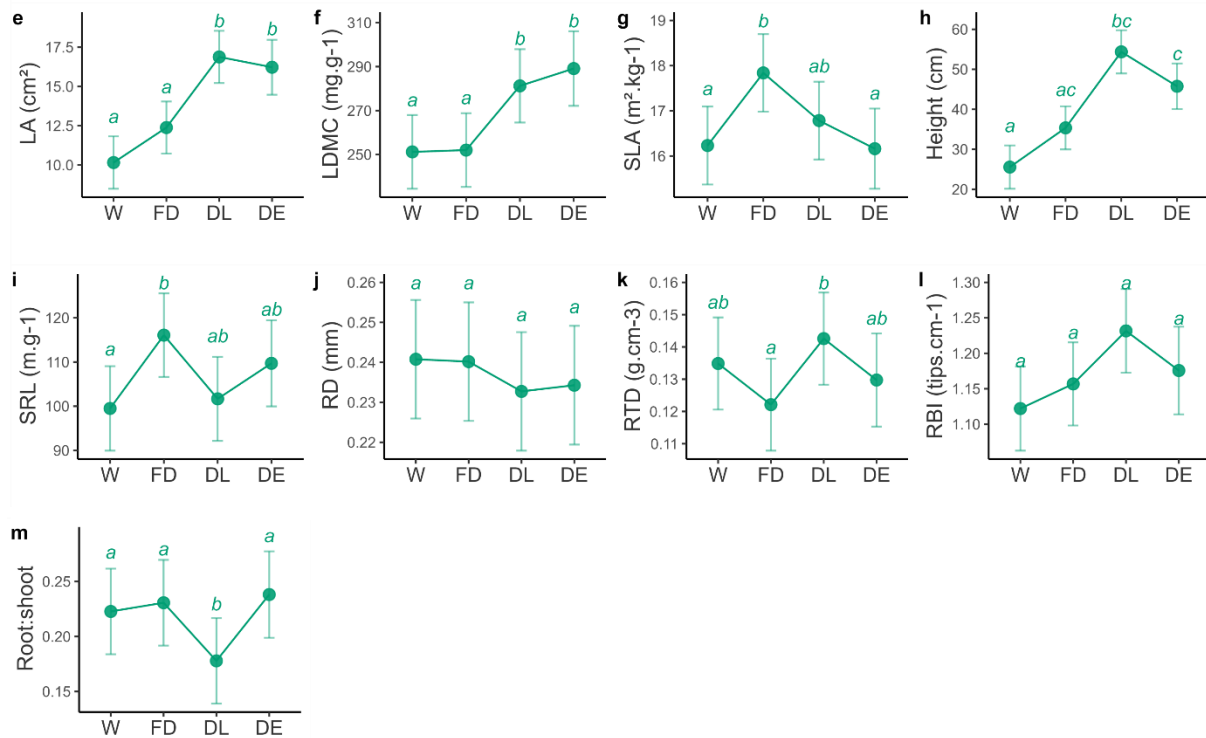


Figure 2. Variation of performance traits (a to d) and functional traits (e to m) of genotypes grown without competition among the four compartments of durum wheat domestication and breeding. Green dots represent mean trait values within domestication compartments. Error bars indicate the mean 95% confidence interval. W, Wild; FD, First domesticated; DL, Durum landrace; DE, Durum elite. a) Log Nb tillers, number of tillers log transformed; b) Aerial biom, vegetative biomass in g; c) Root biom, root biomass in g; d) Total biom, total biomass in g; e) LA, leaf area in cm²; f) LDMC, leaf dry matter content in mg.g⁻¹; g) SLA, specific leaf area in m².kg⁻¹; h) Height, vegetative height before harvest in cm; i) SRL, specific root length in m.g⁻¹; j) RD, mean root diameter in mm; k) RTD, root tissue density in g.cm⁻³; l) RBI, root branching intensity in tips.cm⁻¹; m) Root: shoot, ratio of root biomass on shoot biomass. Letters show significant mean differences between domestication compartments.

Above- and belowground functional traits also varied significantly over the course of domestication and breeding (Fig. 2; Table 1B), except root diameter and RBI (Fig. 2, j, l). Landraces and elite genotypes had a larger leaf area (Fig. 2e) and a higher leaf dry matter content (Fig. 2f) than genotypes from the wild and first domesticated subspecies. Elite and wild genotypes did not differ significantly in their SLA values whereas first domesticated genotypes displayed the highest SLA values (Fig. 2g). Plant height at harvest increased from wild to landraces, with landraces being significantly taller than wild genotypes (Fig. 2h). Although not significant, height decreased between landraces and elite genotypes. SRL and RTD did not show any marked temporal trend; the first domesticated form had the highest SRL and lowest RTD values but did not differ from other compartments (Fig. 2, i, k). Landraces had a root/shoot ratio significantly lower than wild, first domesticated and elite genotypes (Fig. 2m).

Trait response to competition over the course of domestication

Values of performance and functional traits differed significantly between the two competition treatments for all traits, except RBI (Table 1, A, B). In addition, there was a significant interaction between treatment and domestication compartment for all four performance traits (Table 1A: Number of tillers, $P < 0.001$; Aerial biomass, $P < 0.01$; Root biomass, $P < 0.05$; Total biomass, $P = 0.01$) and two functional traits (Table 1B: Root:shoot ratio, $P < 0.001$; Root diameter, $P < 0.001$).

The analysis of R_m based on performance traits showed that the presence of neighbours significantly decreased the number of tillers as well as above- and belowground biomass, and total biomass for all compartments (Fig. 3, a, b, c, d). Yet, the wild compartment showed the strongest decrease in performance traits in response to competition: it significantly lost 62% of its tillers ($P_{W-DL} < 0.01$, $P_{W-DE} < 0.05$; Fig. 3a), 70% of its aerial biomass ($P_{W-FD} < 0.05$, $P_{W-DL} < 0.05$; Fig. 3b), and 69% of its total biomass ($P_{W-FD} < 0.05$; Fig. 3d). Genotypes lost between 56% (DL) and 65% (W and DE genotypes) of their root biomass in response to competition (Fig. 3c).

We found significant differences in R_m between compartments for three functional traits: leaf area, root diameter and root: shoot ratio (Fig. 3, e, j, m). We found that leaf area decreased more strongly in the wild compartment in response to competition than in the other three compartments (Fig. 3e). In addition, wild genotypes significantly increased their root diameter in response to competition compared to the other three compartments (Fig. 3j). We observed a differential response of the root: shoot ratio to competition between compartments both in magnitude and direction: root: shoot

ratio increased in the wild compartment whereas it decreased in the first domesticated form and the elite genotypes (Fig. 3m). Genotypes from all four compartments increased their SLA, and decreased their SRL (Fig. 3, g, i), but no significant differences were observed between compartments.

Lastly, we found that some traits varied in response to competition for some compartments only (Fig. 3). Plant height significantly increased in response to competition in the wild compartment only (Fig. 3h; Table 1B). In addition, we observed little variation of RTD in response to competition, except for elite genotypes (Fig. 3k; Table 1B). The average LDMC and RBI did not vary in one direction in response to competition for any compartment (Fig. 3, f, l).

Table 1. Trait values of performance and functional traits depending on competition treatment (no competition vs competition), compartments (W, FD, DL, DE) and their interactions. A) performance traits: Number of tillers (log transformed), Aerial biomass, Root biomass, and Total biomass; B) functional traits: Root: shoot ratio, Height, Specific leaf area, Leaf area, Leaf dry matter content, Specific root length, Root mean diameter, Root tissue density, and Root branching intensity. Genotype identity nested within compartments and blocks corresponded to random effects. Statistical significance of each term in the model was assessed using Type II analysis of variance with Wald chi-square tests. Significance: ^{NS} P > 0.05; * P < 0.05, ** P < 0.01, *** P < 0.001.

		Fixed effect chisq test				Random effect LRT test			
		<i>N</i>	<i>Treatment</i>	<i>Compartments</i>	<i>Trt</i> * <i>Comp.</i>	<i>ID genotype</i>	<i>Block</i>	<i>R</i> ² <i>marginal</i>	<i>R</i> ² <i>conditional</i>
A - Performance traits	Number tillers (log)	304	391.3***	8.8*	29.1***	80.6***	1.4 ^{NS}	0.48	0.70
	Aerial biomass	297	503.3***	68.8***	12.3**	19.3***	0.3 ^{NS}	0.66	0.72
	Root Biomass	298	730.3***	17.9***	10.9*	34.6***	12.0***	0.66	0.76
	Total biomass	294	637.8***	63.9***	11.2*	18.9***	0.3 ^{NS}	0.70	0.75
B - Functional traits	Root:shoot	294	7.5**	14.2**	49.9***	53.6***	17.1***	0.21	0.51
	Height	303	6.4**	73.6***	1.5 ^{NS}	157.8***	0 ^{NS}	0.55	0.81
	LA	304	121.9***	51.8***	5.1 ^{NS}	117.4***	0 ^{NS}	0.49	0.75
	SLA	304	188.4***	17.6***	1.8 ^{NS}	33.1***	4.3*	0.38	0.54
	LDMC	294	4.9*	36.6***	6.4 ^{NS}	26.8***	17.5***	0.24	0.46
	SRL	300	52.5***	16.3***	4.5 ^{NS}	17.7***	3.5 ^{NS}	0.21	0.36
	RD	303	37.9***	18.4***	19.7***	17.2***	25.3***	0.2	0.41
	RTD	301	8.6**	12.8**	4.6 ^{NS}	45.5***	47.5***	0.12	0.48
RBI	303	3.8 ^{NS}	5.5 ^{NS}	5.6 ^{NS}	43.2***	87.4***	0.05	0.51	

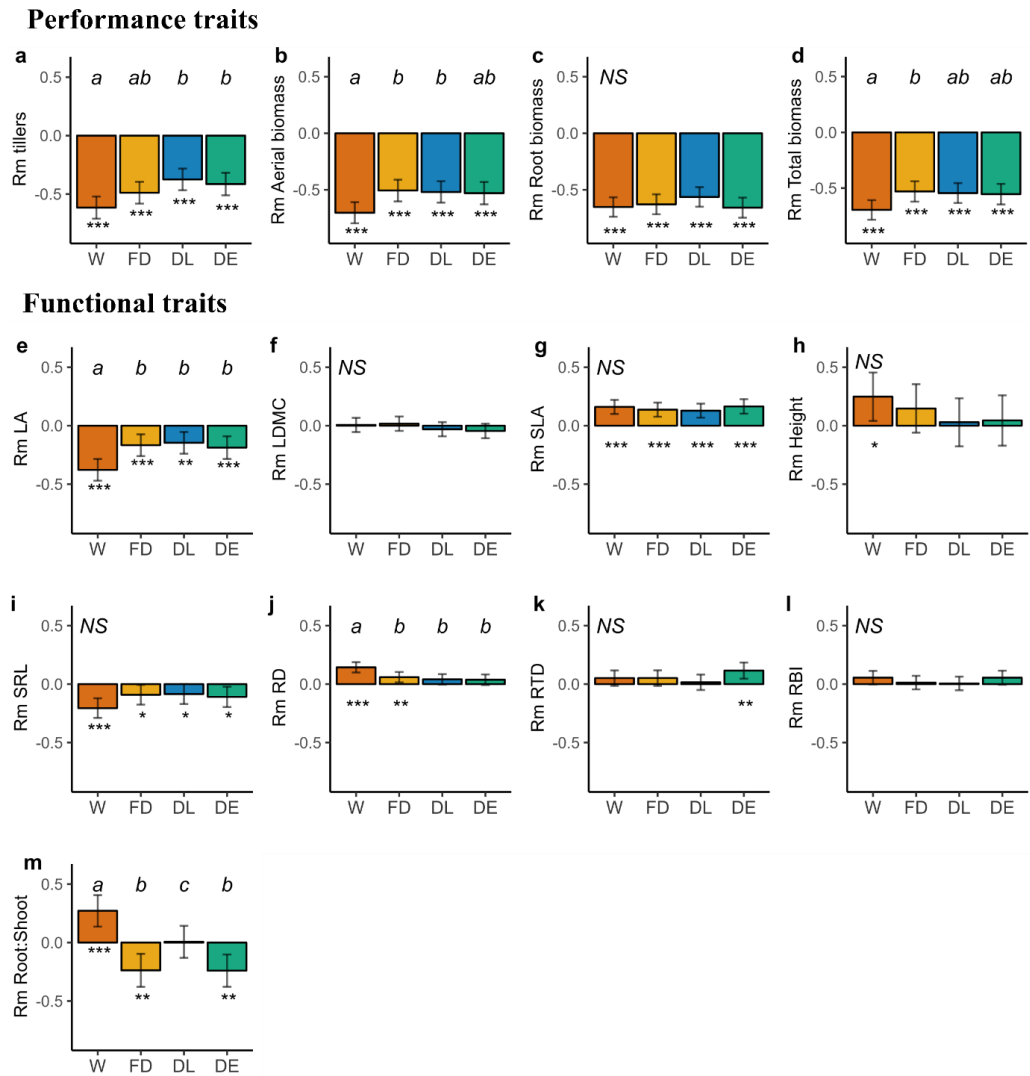


Figure 3. Variation in trait response to competition measured as the competitive response index R_m for wheat genotypes belonging to different domestication stages, for both performance and functional traits. R_m is averaged among genotypes within compartment. Negative values of R_m indicate that the trait value in competition is smaller than in the isolated condition. W, Wild; FD, First domesticated; DL, Durum landrace; DE, Durum elite. Error bars indicate mean 95% confidence intervals. a) tillers, number of tillers; b) Aerial biomass, vegetative biomass in g; c) Root biomass, root biomass in g; d) Total biomass, total biomass in g; e) LA, leaf area in cm^2 ; f) LDMC, leaf dry matter content in mg.g^{-1} ; g) SLA, specific leaf area in $\text{m}^2.\text{kg}^{-1}$; h) Height, vegetative height before harvest in cm; i) SRL, specific root length in m.g^{-1} ; j) RD, mean root diameter in mm; k) RTD, root tissue density in g.cm^{-3} ; l) RBI, root branching intensity in tips.cm^{-1} ; m) Root/shoot, root: shoot ratio. Different letters show significant mean differences between compartments. Stars indicate values of R_m significantly different from 0 within compartment. Significance, ^{NS} $P > 0.05$; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Is plant response to competition explained by trait values and phenotypic plasticity?

Overall, no relationship was detected between plant response to competition (R_m) based on total biomass and above- or belowground functional trait values measured on plants in isolated conditions (Table S2; Fig. 4; Fig. 5). This relationship was only significant for leaf area and height in the wild compartment, where plants with larger leaf area and taller plants showed a lower performance under competition (Fig. 4, a, j; Table S2).

For each compartment, significant relationships were detected between plant response to competition and, respectively, focal leaf area and height values measured on plants in the competition treatment. Moreover, these relationships were of opposite sign compared to those found in isolated condition (Fig. 4, b, k; Table S3). Genotypes with a larger leaf area in the competition treatment performed better under competition ($R^2 = 0.27$; $P_{all} < 0.001$; Fig. 4b; Table S3). Additionally, taller plants in the competition treatment performed better under competition ($R^2 = 0.20$; $P_{all} < 0.001$; Fig. 4k; Table S3). We did not detect significant differences in slope for leaf area and height between compartments.

Aboveground response of functional traits to competition significantly modulated the performance of plants submitted to competition (Fig. 4; Table S4). Indeed, when plants increased their leaf area and height in response to competition, they performed better under competition (Fig. 4, c, l). For leaf area, the relationship was significant both within each compartment and when pooling data across compartments ($P < 0.001$; Fig 4c; Table S4). For height, the relationship was significant for each compartment, except for the elite one ($P_W = 0.001$, $P_{FD} < 0.001$, $P_{DL} < 0.001$; Fig 4l; Table S4). The slope of the relationship between plant performance under competition and height plasticity was significantly higher in landraces ($\beta = 0.61$) compared to the wild compartment ($\beta = 0.14$). This means that the same investment in plasticity contributed less to the performance under competition for wild genotypes compared to landraces ($P < 0.01$; Table S4). Genotypes that increased their SLA in response to competition suffered the most from competition ($R^2 = 0.07$; $P_{all} < 0.01$; Fig. 4i).

R_m based on total biomass was not correlated to belowground trait values in isolated conditions or in competition, as well as to belowground traits plasticity, except for root diameter and root: shoot ratio (Fig. 5). Indeed, landraces with thicker roots in response to competition performed worse under competition ($P < 0.05$; Fig 5c; Table S4). Additionally, we found that genotypes with higher

values of root: shoot in competition treatment, i.e. higher investment in root biomass, were less performant under competition (Fig 5n). The relationship was significant within the wild compartment ($P < 0.05$; Fig 5n; Table S3). Moreover, when plants increased their root: shoot in response to competition, they were less performant under competition (Fig 5o; Table S4).

Finally, we detected significant differences in mean C-scores between compartments, only when scores were calculated with trait values measured on plants in the competition treatment (Fig. 6a). In the competition treatment, the wild compartment had the lowest C-score compared to landraces and elite genotypes ($P_{W-DL} < 0.001$, $P_{W-DE} < 0.05$; Fig. 6a). C-scores based on traits measured in competition were significantly and positively related to plant performance under competition at the whole dataset level ($R^2 = 0.22$; $P_{all} < 0.001$; Fig. 6, b, c) and within each of the four compartments ($P < 0.001$). Focal plants with a low competitive score in competition treatment suffered the most from competition.

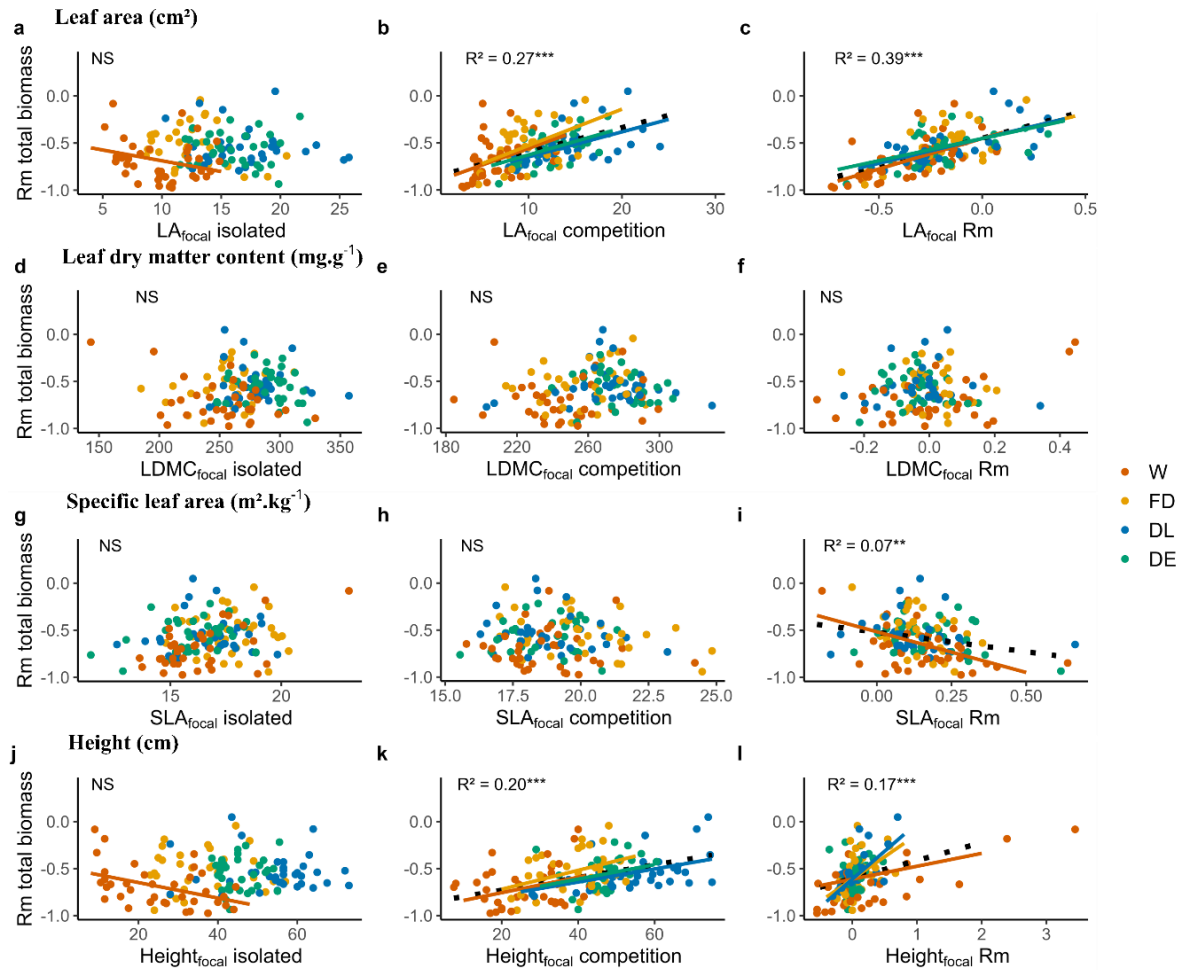


Figure 4. Effects of aboveground trait values of the focal plant in (1) isolated treatment, (2) in competition treatment and of (3) focal competitive response based on aboveground functional traits (R_m) on focal competitive response index based on total biomass (R_m). a to c) LA, leaf area in cm^2 ; d to f) LDMC, leaf dry matter content in $\text{mg}\cdot\text{g}^{-1}$; g to i) SLA, specific leaf area in $\text{m}^2\cdot\text{kg}^{-1}$; j to l) Height, vegetative height before harvest in cm. Negative values of competitive response index indicate that the focal trait value in competition was smaller than in isolated conditions. Regression lines were obtained from a linear mixed model, see Table S2, and are only displayed when the relationship is significant. Black dotted line shows the regression line when pooling data over compartments (Adjusted coefficient of determination R^2 marginal is given). The coloured dots and lines correspond to the different compartments: Wild (Red), First domesticated (Orange), Durum landrace (Blue) and Durum elite (Green). Significance: ^{NS} $P > 0.05$; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

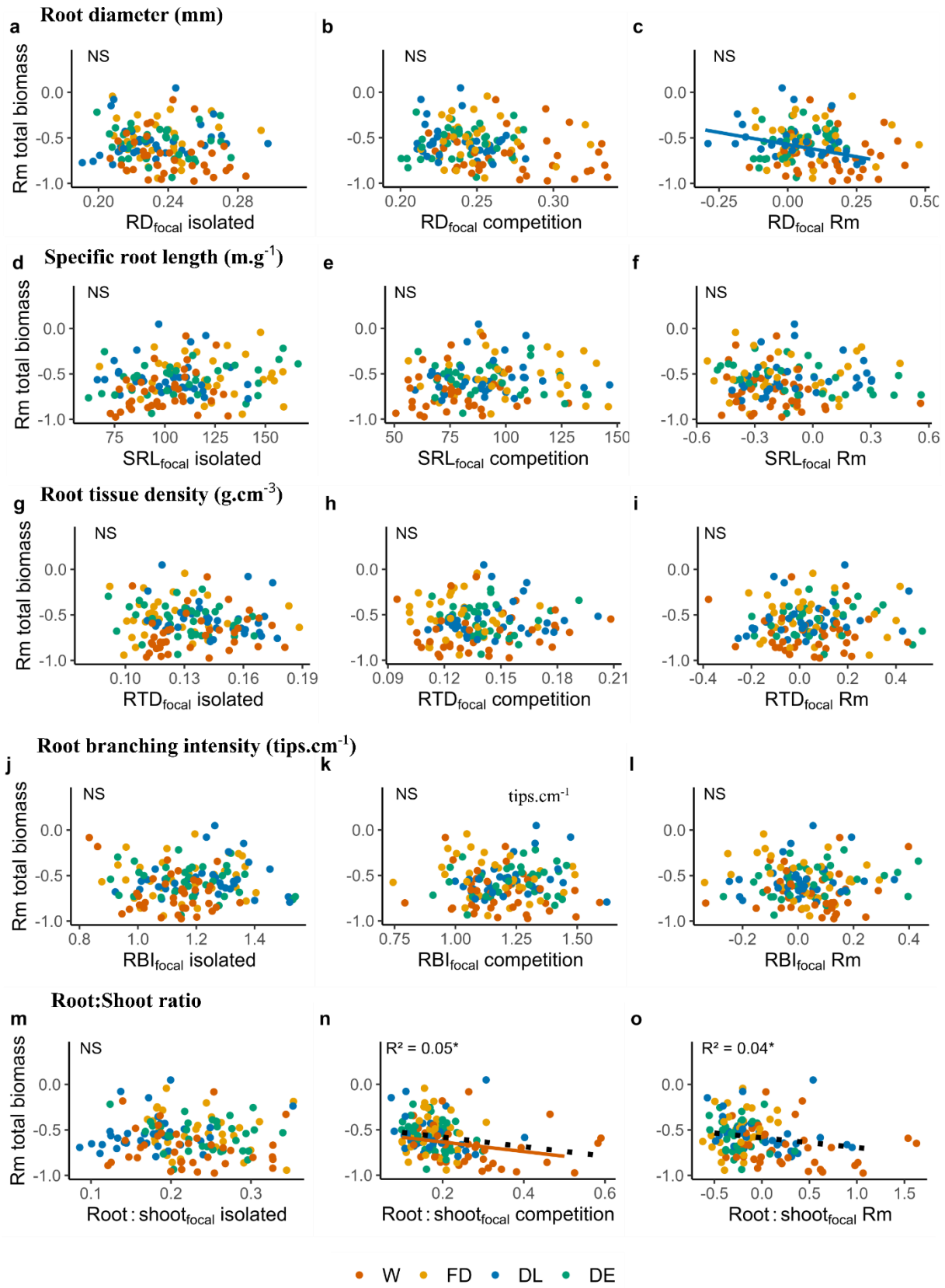


Figure 5. Effects of belowground trait values of the focal plant in (1) isolated treatment, (2) in competition treatment and of (3) focal trait competitive response based on belowground functional traits (R_m) on focal competitive response index based on total biomass (R_m). a to c) RD, mean root diameter in mm; d to f) SRL, specific root length in m.g^{-1} ; g to i) RTD, root tissue density in g.cm^{-3} ; j to l) RBI, root branching intensity in tips.cm^{-1} ; m to o) Root: shoot, root: shoot ratio. Negative values of competitive response index indicate that the focal trait value in competition is smaller than in isolated conditions. Regression lines were obtained from a linear mixed model, see Table S2, and are only displayed when the relationship is significant. Adjusted coefficient of determination R^2 marginal is given. The coloured dots and lines correspond to the different compartments: Wild (Red), First domesticated (Orange), Durum landrace (Blue) and Durum elite (Green). Significance: ^{NS} $P > 0.05$; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

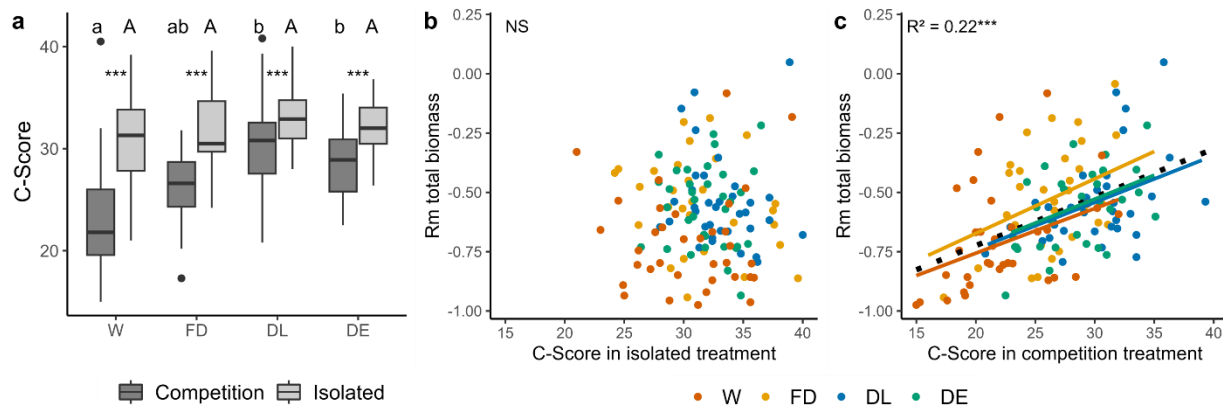


Figure 6. a) Comparison of C-scores of each focal plant estimated from combinations of leaf traits within the triangle of CSR strategies (Pierce *et al.*, 2017) between compartments and treatments. Different capital letters show significant mean differences between compartments in isolated conditions. Different lowercase letters show significant mean differences between compartments in competition conditions. Stars indicate significant mean differences between treatment in each compartment. b, c) Relationships between C-scores of each focal plant and the competitive response of focal plant based on total biomass (R_m). b) Traits in isolated treatment; c) Traits in competition treatment. Negative values of competitive response index indicate that the focal trait value in competition is smaller than in isolated conditions. Black dotted line shows the regression line when pooling data over compartments (Adjusted coefficient of determination R^2 marginal is given). Significance: ^{NS} $P > 0.05$; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

VII. Discussion

In this study, we documented phenotypic changes throughout the process of domestication and breeding of durum wheat. We found that domesticated forms performed better under competition compared to their wild progenitors in spite of the lower level of phenotypic plasticity expressed by those domesticated plants. Importantly, we identified a small set of plant traits measured under competition that captured plant's response to competition.

In this study, we demonstrated a change in the response to competition between wild ancestors and domesticated forms. We highlighted that the response to competition did not vary between domesticated forms (early domesticated forms, landraces, modern forms). On the other hand, we found that wild forms performed less well under competition than early domesticated forms. These findings suggest that unintended selection due to competitive environmental conditions within agroecosystems have probably led wheat from the early stages of domestication, to adapt to competition and performed better under competition than wild forms. Indeed, cultivation practices have created new, disturbed, nutrient-rich habitats open to competition with other species and increasingly densely populated (Chapin, 1980; Milla *et al.*, 2015; Fuller & Stevens, 2017; Milla, 2023). These conditions have favoured genotypes that possessed traits that gave them a competitive advantage (Fuller *et al.*, 2010; Fuller & Stevens, 2017; Preece *et al.*, 2021). Here, we highlighted an increase in plant height, plant biomass, shoot biomass investment and leaf area during domestication, providing a competitive advantage for light capture in dense field. This finding highlights that evolution of crops has gradually led to changes in phenotype characterizing stronger competitors for light. An increase in plant size (Milla *et al.*, 2014; Milla & Matesanz, 2017) and seed size (Purugganan & Fuller, 2009; Preece *et al.*, 2021), two key competition related traits (Weiner, 1990), has been reported in other crop species over the course of domestication. We also found changes in root traits with a significant increase in specific root length and a decrease in root tissue density from the wild to the first domesticated forms of wheat. These findings suggest a shift, at the beginning of domestication, towards faster acquisition strategies of soil resources, which have been shown to be associated to higher competitive ability in wild species (Mommer *et al.*, 2011).

Genotypes' trait values in isolated conditions do not explain ability of plants to perform in response to competition, except for the wild compartment. As an example, tall wild genotypes and wild

genotypes with large leaf area in isolated conditions lost more total biomass under competition, suggesting that there might be a cost to investing in one's vegetative structure as one may lose more in competition. At the intraspecific level, plant traits of isolated plants do not seem relevant proxies of their competitive response, which could be explained by the interplay with trait plasticity (Crick & Grime, 1987; Callaway *et al.*, 2003; Novoplansky, 2009) and the trait values of the competing phenotype (Gaudet & Keddy, 1988; Violle *et al.*, 2009; Kunstler *et al.*, 2016). Conversely, we found that leaf area and height of plants in the competition treatment were related to their ability to tolerate competition, suggesting that traits allowing greater light interception by the focal plant allow it to better tolerate competition for resources. This finding agrees with other studies showing that several aboveground traits such as large plant size and leaf acquisitive traits reduce plant biomass loss under competition (e.g., Gaudet & Keddy, 1988; Goldberg & Landa, 1991; Keddy *et al.*, 2002; Bennett *et al.*, 2016). This result is reinforced by the positive relation between C-score and competitive response: the genotypes with highest C-score lost less total biomass in response to competition. In our study, we showed that C-score in isolated conditions (Grime, 1977) did not reflect the plants' ability to respond to competition, probably because of the context-dependence of the traits. The C-score is therefore a relevant indicator of plant response and should be measured under real-life conditions. Surprisingly, we did not find any effect of root traits on plant performance under competition, conversely to interspecific studies (e.g., Fargione & Tilman, 2006; Fort *et al.*, 2014; Semchenko *et al.*, 2018). We only found that genotypes, and in particular wild progenitors, which invested more biomass in root compartment were less performant under competition. This may reflect higher but maladaptive investment in response to underground competition. Indeed, genotypes lost a large part of their root biomass in competition, preventing them from occupying a large competing soil space (Semchenko *et al.*, 2018). We can however underline a limit of the study related to the pot experimentation (Freschet *et al.*, 2021), which undoubtedly limited the expression of potential root strategies involved in plant response to competition.

We detected a common pattern of wheat varieties in response to competition: they built cheaper leaves (lower leaf area, higher specific leaf area; shade response e.g., Valladares & Niinemets, 2008) and invested in a less extensive root systems (lower specific root length and higher root diameter). Interestingly, we observed significant differences in plasticity between domesticated forms and the wild compartment. Wild genotypes showed a significant decrease in their leaf area

and a significant increase in their average root diameter in response to competition, reflecting a whole-plant scale reduction in plant organ structure and carbon cost. As such, leaf area and specific root length plasticity of genotypes could result from adjustments in phenotypic development, as a cause or a consequence of changes in plant biomass with resource depletion (Weiner, 2004). In cross-species comparisons, some studies also reported an increase in root diameter and a decrease in specific root length in response to competition, considered as a shift towards more stress-tolerant strategies, i.e. a competitive avoidance (Bennett *et al.*, 2016) or tolerance (Wang *et al.*, 2010; Semchenko *et al.*, 2018) strategy. Conversely, other works showed a more confrontational response to competition: plants increased light interception and nutrient acquisition through larger leaves (Aphalo *et al.*, 1999; Valladares *et al.*, 2000; Vermeulen *et al.*, 2008) and shifted root traits towards nutrient-acquiring strategies (Borden *et al.*, 2020). Interestingly, we detected a significant directional plant height plasticity in response to competition in the wild compartment only. Height convergence in the elite compartment, due to the introgression of the dwarfism gene, has probably led to counter-selection of height plasticity in response to neighbourhood, as already discussed in wheat (Sadras *et al.*, 2011; Colombo *et al.*, 2022). Whatever the level of phenotypic plasticity expressed by the studied genotypes, we found significant relationships between phenotypic plasticity - based on height, specific leaf area or leaf area - and plant performance across domestication compartments. More precisely, when a plant increased its leaf area and height and decreased its specific leaf area in the competition treatment, it experienced lower performance declines when grown under competition. This suggests that genotypes take advantage of the plasticity of aboveground traits, which is a way to cope with competition for light. This has already been shown in intercropping annual species, for which plasticity of several aboveground traits was related to improved light availability and increase yield (Zhu *et al.*, 2015, 2016). Height plasticity hardly varied among durum elite genotypes, which could explain the absence of relationship between plant height and competitive response for this domestication compartment.

Our findings highlighted that domesticated forms of wheat performed better under competition than their wild progenitors, thus confirming the effect of domestication and breeding on crop adaptation to competition. Although the wild compartment showed the strongest directional plastic response to competition for several traits, plasticity of leaf and root traits still exists in modern compartments, which can be considered as a promising target for future breeding programs (Litrico

& Violle 2015). We found that traits measured in competitive conditions explain a significant part of plants performance under competition (Violle *et al.*, 2009). Phenotypic plasticity can thus play an important role in the variation of plant performance (MacLaren *et al.*, 2023).

VIII. Acknowledgements

We thank the TE platform team of the LabEx CeMEB for providing all the facilities and technical support. Experimental work was supported by the Agence Nationale de la Recherche (ANR) project “Selecting for cooperative crops to develop sustainable agriculture” (SCOOP, grant no. ANR-19-CE32-0011).

IX. Author contributions

CV, HF, FF, and TL, planned and designed the research. EG, MG and TL performed the experiment. TL analysed the data. TL, CV, FF and HF wrote the first version of the manuscript. All authors read and approved the final manuscript.

X. Data availability

The data to reproduce all analyses of this paper can be accessed at [to be completed upon final acceptance].

XI. References

Anten NPR, Vermeulen PJ. 2016. Tragedies and Crops: Understanding Natural Selection To Improve Cropping Systems. *Trends in Ecology & Evolution* **31**: 429–439.

Aphalo PJ, Ballare CL, Scopel AL. 1999. Plant–plant signalling, the shade-avoidance response and competition. *Journal of Experimental Botany* **50**: 1629-1634,.

Bennett JA, Riibak K, Tamme R, Lewis RJ, Pärtel M. 2016. The reciprocal relationship between competition and intraspecific trait variation. *Journal of Ecology* **104**: 1410–1420.

- Biernaskie JM. 2022.** Kin selection theory and the design of cooperative crops. *Evolutionary Applications* **15**: 1555–1564.
- Borden KA, Thomas SC, Isaac ME. 2020.** Variation in fine root traits reveals nutrient-specific acquisition strategies in agroforestry systems. *Plant and Soil* **453**: 139–151.
- Bret-Harte MS, Shaver GR, Zoerner JP, Johnstone JF, Wagner JL, Chavez AS, Gunkelman IV RF, Lippert SC, Laundre JA. 2001.** Developmental Plasticity Allows *Betula Nana* to Dominate Tundra Subjected to an Altered Environment. *Ecology* **82**: 18–32.
- Cahill JF, Lamb EG. 2007.** Interactions Between Root and Shoot Competition and Plant Traits. *HortScience* **42**: 1110–1112.
- Callaway RM, Pennings SC, Richards CL. 2003.** Phenotypic Plasticity and Interactions Among Plants. *Ecology* **84**: 1115–1128.
- Chapin FS. 1980.** The Mineral Nutrition of Wild Plants. *Annual Review of Ecology and Systematics* **11**: 233–260.
- Chen YH, Gols R, Benrey B. 2015.** Crop Domestication and Its Impact on Naturally Selected Trophic Interactions. *Annual Review of Entomology* **60**: 35–58.
- Colombo M, Montazeaud G, Viader V, Ecartot M, Prosperi J-M, David J, Fort F, Violle C, Fréville H. 2022.** A genome-wide analysis suggests pleiotropic effects of Green Revolution genes on shade avoidance in wheat. *Evolutionary Applications* **15**: 1594–1604.
- Crick J c., Grime J p. 1987.** Morphological Plasticity and Mineral Nutrient Capture in Two Herbaceous Species of Contrasted Ecology. *New Phytologist* **107**: 403–414.
- Denison RF. 2015.** Evolutionary tradeoffs as opportunities to improve yield potential. *Field Crops Research* **182**: 3–8.
- Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Colin Prentice I, et al. 2016.** The global spectrum of plant form and function. *Nature* **529**: 167–171.
- Donald CM. 1963.** Competition Among Crop and Pasture Plants. In: Norman AG, ed. *Advances in Agronomy*. Academic Press, 1–118.
- Donald CM. 1968.** The breeding of crop ideotypes. *Euphytica* **17**: 385–403.
- Fargione J, Tilman D. 2006.** Plant species traits and capacity for resource reduction predict yield and abundance under competition in nitrogen-limited grassland. *Functional Ecology* **20**: 533–540.
- Fort F, Cruz P, Jouany C. 2014.** Hierarchy of root functional trait values and plasticity drive early-stage competition for water and phosphorus among grasses. *Functional Ecology* **28**: 1030–1040.
- Foster BL. 2000.** Competition at the population level along a standing crop gradient: a field experiment in successional grassland. *Plant Ecology* **151**: 171–180.
- Freschet GT, Pagès L, Iversen CM, Comas LH, Rewald B, Roumet C, Klimešová J, Zadworny M, Poorter H, Postma JA, et al. 2021.** A starting guide to root ecology: strengthening ecological concepts and

standardising root classification, sampling, processing and trait measurements. *New Phytologist* **232**: 973–1122.

Fréville H, Montazeaud G, Forst E, David J, Papa R, Tenailon MI. 2022. Shift in beneficial interactions during crop evolution. *Evolutionary Applications* **15**: 905–918.

Fuller DQ, Allaby RG, Stevens C. 2010. Domestication as innovation: the entanglement of techniques, technology and chance in the domestication of cereal crops. *World Archaeology* **42**: 13–28.

Fuller DQ, Denham T, Arroyo-Kalin M, Lucas L, Stevens CJ, Qin L, Allaby RG, Purugganan MD. 2014. Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record. *Proceedings of the National Academy of Sciences* **111**: 6147–6152.

Fuller DQ, Stevens CJ. 2017. Open for Competition: Domesticates, Parasitic Domesticoids and the Agricultural Niche. *Archaeology International* **20**.

Funk JL, Wolf AA. 2016. Testing the trait-based community framework: Do functional traits predict competitive outcomes? *Ecology* **97**: 2206–2211.

Gaudet CL, Keddy PA. 1988. A comparative approach to predicting competitive ability from plant traits. *Nature* **334**: 242–243.

Gioia T, Nagel KA, Beleggia R, Fragasso M, Ficco DBM, Pieruschka R, De Vita P, Fiorani F, Papa R. 2015. Impact of domestication on the phenotypic architecture of durum wheat under contrasting nitrogen fertilization. *Journal of Experimental Botany* **66**: 5519–5530.

Goldberg D. 1990. Components of resource competition in plant communities. In: Perspectives on plant competition. 27–49.

Goldberg DE, Fleetwood L. 1987. Competitive Effect and Response in Four Annual Plants. *The Journal of Ecology* **75**: 1131.

Goldberg DE, Landa K. 1991. Competitive Effect and Response: Hierarchies and Correlated Traits in the Early Stages of Competition. *Journal of Ecology* **79**: 1013–1030.

Goldberg E, Werner PA. 1983. Equivalence of Competitors in Plant Communities: A Null Hypothesis and a Field Experimental Approach. *American Journal of Botany* **70**: 1098–1104.

Grams TEE, Andersen CP. 2007. Competition for Resources in Trees: Physiological Versus Morphological Plasticity. In: Esser K, Löttge U, Beyschlag W, Murata J, eds. Progress in Botany. Progress in Botany. Berlin, Heidelberg: Springer, 356–381.

Grime JP. 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist* **111**: 1169–1194.

Grime JP, Hunt R. 1975. Relative Growth-Rate: Its Range and Adaptive Significance in a Local Flora. *Journal of Ecology* **63**: 393–422.

Harlan JR, de Wet JMJ, Price EG. 1973. Comparative Evolution of Cereals. *Evolution* **27**: 311–325.

- Isaac ME, Nimmo V, Gaudin ACM, Leptin A, Schmidt JE, Kallenbach CM, Martin A, Entz M, Carkner M, Rajcan I, et al. 2021.** Crop Domestication, Root Trait Syndromes, and Soil Nutrient Acquisition in Organic Agroecosystems: A Systematic Review. *Frontiers in Sustainable Food Systems* **5**: 716480.
- Kebrom TH, Brutnell TP. 2007.** The molecular analysis of the shade avoidance syndrome in the grasses has begun. *Journal of Experimental Botany* **58**: 3079–3089.
- Keddy PA. 1992.** A Pragmatic Approach to Functional Ecology. *Functional Ecology* **6**: 621.
- Keddy P, Fraser LH, Wisheu IC. 1998.** A comparative approach to examine competitive response of 48 wetland plant species. *Journal of Vegetation Science* **9**: 777–786.
- Keddy P, Nielsen K, Weiher E, Lawson R. 2002.** Relative competitive performance of 63 species of terrestrial herbaceous plants. *Journal of Vegetation Science* **13**: 5–16.
- Keddy PA, Shipley B. 1989.** Competitive Hierarchies in Herbaceous Plant Communities. *Oikos* **54**: 234–241.
- Kunstler G, Falster D, Coomes DA, Hui F, Kooyman RM, Laughlin DC, Poorter L, Vanderwel M, Vieilledent G, Wright SJ, et al. 2016.** Plant functional traits have globally consistent effects on competition. *Nature* **529**: 204–207.
- Martín-Robles N, Morente-López J, Freschet GT, Poorter H, Roumet C, Milla R. 2019.** Root traits of herbaceous crops: Pre-adaptation to cultivation or evolution under domestication? *Functional Ecology* **33**: 273–285.
- Meyer RS, DuVal AE, Jensen HR. 2012.** Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops. *New Phytologist* **196**: 29–48.
- Milla R. 2023.** Phenotypic evolution of agricultural crops. *Functional Ecology* **37**: 976–988.
- Milla R, Matesanz S. 2017.** Growing larger with domestication: a matter of physiology, morphology or allocation? *Plant Biology* **19**: 475–483.
- Milla R, Morente-López J, Alonso-Rodrigo JM, Martín-Robles N, Stuart Chapin F. 2014.** Shifts and disruptions in resource-use trait syndromes during the evolution of herbaceous crops. *Proceedings of the Royal Society B: Biological Sciences* **281**: 20141429.
- Milla, Osborne CP, Turcotte MM, Violle C. 2015.** Plant domestication through an ecological lens. *Trends in Ecology & Evolution* **30**: 463–469.
- Mommer L, Visser EJW, van Ruijven J, de Caluwe H, Pierik R, de Kroon H. 2011.** Contrasting root behaviour in two grass species: a test of functionality in dynamic heterogeneous conditions. *Plant and Soil* **344**: 347–360.
- Montazeaud G, Rousset F, Fort F, Violle C, Fréville H, Gandon S. 2020.** Farming plant cooperation in crops. *Proceedings of the Royal Society B: Biological Sciences* **287**: 20191290.
- Navas M-L, Garnier E. 2002.** Plasticity of whole plant and leaf traits in *Rubia peregrina* in response to light, nutrient and water availability. *Acta Oecologica* **23**: 375–383.

Novoplansky A. 2009. Picking battles wisely: plant behaviour under competition. *Plant, Cell & Environment* **32**: 726–741.

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, et al. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* **61**: 167.

Pierce S, Negreiros D, Cerabolini BEL, Kattge J, Díaz S, Kleyer M, Shipley B, Wright SJ, Soudzilovskaia NA, Onipchenko VG, et al. 2017. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology* **31**: 444–457.

Preece C, Jones G, Rees M, Osborne CP. 2021. Fertile Crescent crop progenitors gained a competitive advantage from large seedlings. *Ecology and Evolution* **11**: 3300–3312.

Purugganan MD, Fuller DQ. 2009. The nature of selection during plant domestication. *Nature* **457**: 843–848.

Reich PB. 2014. The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**: 275–301.

Roucou A, Violle C, Fort F, Roumet P, Ecartot M, Vile D. 2018. Shifts in plant functional strategies over the course of wheat domestication. *Journal of Applied Ecology* **55**: 25–37.

Sadras VO, Lawson C, Sadras VO, Lawson C. 2011. Genetic gain in yield and associated changes in phenotype, trait plasticity and competitive ability of South Australian wheat varieties released between 1958 and 2007. *Crop and Pasture Science* **62**: 533–549.

Schenk HJ. 2006. Root competition: beyond resource depletion. *Journal of Ecology* **94**: 725–739.

Semchenko M, Lepik A, Abakumova M, Zobel K. 2018. Different sets of belowground traits predict the ability of plant species to suppress and tolerate their competitors. *Plant and Soil* **424**: 157–169.

Sorrensen-Cothorn KA, Ford ED, Sprugel DG. 1993. A Model of Competition Incorporating Plasticity through Modular Foliage and Crown Development. *Ecological Monographs* **63**: 277–304.

Spor A, Roucou A, Mounier A, Bru D, Breuil M-C, Fort F, Vile D, Roumet P, Philippot L, Violle C. 2020. Domestication-driven changes in plant traits associated with changes in the assembly of the rhizosphere microbiota in tetraploid wheat. *Scientific Reports* **10**: 12234.

Tanno K, Willcox G. 2012. Distinguishing wild and domestic wheat and barley spikelets from early Holocene sites in the Near East. *Vegetation History and Archaeobotany* **21**: 107–115.

Turcotte MM, Turley NE, Johnson MTJ. 2014. The impact of domestication on resistance to two generalist herbivores across 29 independent domestication events. *New Phytologist* **204**: 671–681.

Valladares F, Gianoli E, Gómez JM. 2007. Ecological limits to plant phenotypic plasticity. *New Phytologist* **176**: 749–763.

Valladares F, Martinez-Ferri E, Balaguer L, Perez-Corona E, Manrique E. 2000. Low leaf-level response to light and nutrients in Mediterranean evergreen oaks: a conservative resource-use strategy? *The New Phytologist* **148**: 79–91.

Valladares F, Niinemets Ü. 2008. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. *Annual Review of Ecology, Evolution, and Systematics* **39**: 237–257.

Vermeulen PJ, Anten NPR, Schieving F, Werger MJA, During HJ. 2008. Height convergence in response to neighbour growth: genotypic differences in the stoloniferous plant *Potentilla reptans*. *New Phytologist* **177**: 688–697.

Violle C, Garnier E, Lecoœur J, Roumet C, Pouteau C, Blanchard A, Navas M-L. 2009. Competition, traits and resource depletion in plant communities. *Oecologia* **160**: 747–755.

Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! *Oikos* **116**: 882–892.

Wang P, Stieglitz T, Zhou DW, Cahill Jr JF. 2010. Are competitive effect and response two sides of the same coin, or fundamentally different? *Functional Ecology* **24**: 196–207.

Weiner J. 1990. Asymmetric competition in plant populations. *Trends in Ecology & Evolution* **5**: 360–364.

Weiner J. 2004. Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics* **6**: 207–215.

Weiner J. 2019. Looking in the Wrong Direction for Higher-Yielding Crop Genotypes. *Trends in Plant Science* **24**: 927–933.

Welcker C, Spencer NA, Turc O, Granato I, Chapuis R, Madur D, Beauchene K, Gouesnard B, Draye X, Palaffre C, et al. 2022. Physiological adaptive traits are a potential allele reservoir for maize genetic progress under challenging conditions. *Nature Communications* **13**: 3225.

Wuest SE, Peter R, Niklaus PA. 2021. Ecological and evolutionary approaches to improving crop variety mixtures. *Nature Ecology & Evolution*.

Zhu J, van der Werf W, Anten NPR, Vos J, Evers JB. 2015. The contribution of phenotypic plasticity to complementary light capture in plant mixtures. *New Phytologist* **207**: 1213–1222.

Zhu J, van der Werf W, Vos J, Anten N p. r., van der Putten P e. l., Evers J b. 2016. High productivity of wheat intercropped with maize is associated with plant architectural responses. *Annals of Applied Biology* **168**: 357–372.

SUPPLEMENTARY INFORMATION

Domesticated plants performed better under competition than their wild progenitors despite lower phenotypic plasticity

XII. Supporting Information

Table S1. List of accessions. Seeds were provided by INRAE UMR AGAP in Montpellier, France.

INRAE accession number	International accession number	Collection	Compartment
48	46499	Icarda	<i>dicoccoides</i>
50	46491	Icarda	<i>dicoccoides</i>
62	46309	Icarda	<i>dicoccoides</i>
63	46310	Icarda	<i>dicoccoides</i>
71	46453	Icarda	<i>dicoccoides</i>
73	46253	Icarda	<i>dicoccoides</i>
75	116179	Icarda	<i>dicoccoides</i>
83	466987	USDA	<i>dicoccoides</i>
85	467014	USDA	<i>dicoccoides</i>
90	352324	USDA	<i>dicoccoides</i>
116	45383	Icarda	<i>dicoccum</i>
128	45351	Icarda	<i>dicoccum</i>
130	45239	Icarda	<i>dicoccum</i>
137	45354	Icarda	<i>dicoccum</i>
139	45280	Icarda	<i>dicoccum</i>
143	45441	Icarda	<i>dicoccum</i>
157	352365	USDA	<i>dicoccum</i>
184	415152	USDA	<i>dicoccum</i>
202	319868	USDA	<i>dicoccum</i>
208	cwi17084	CIMMYT	<i>dicoccum</i>
250	edmore (495)	montpellier	<i>durum</i>
302	84866	Icarda	<i>durum</i>
312	97512	Icarda	<i>durum</i>
328	95920	Icarda	<i>durum</i>
344	82697	Icarda	<i>durum</i>
346	82702	Icarda	<i>durum</i>
349	82768	Icarda	<i>durum</i>
351	82726	Icarda	<i>durum</i>
354	82715	Icarda	<i>durum</i>
362	AGATHE	GEVES	<i>durum</i>
374	DURGAMM	GEVES	<i>durum</i>
380	NITA	GEVES	<i>durum</i>
382	ROMEO	GEVES	<i>durum</i>
395	PRIMADUR	GEVES	<i>durum</i>
405	ARBOIS	GEVES	<i>durum</i>
411	NEODUR	GEVES	<i>durum</i>
430	IXOS	GEVES	<i>durum</i>
437	DURENTAL	GEVES	<i>durum</i>
581	B6R	(maria)	<i>durum</i>

Table S2. Linear mixed model results presenting the effects of trait values of the focal plant in isolated treatment on focal competitive response. “All” correspond to results of a linear mixed model where data of all the compartments were pooled. The lines containing the four domestication compartments correspond to the results of nested linear mixed models. Genotype identity nested in domestication compartments and block position correspond to random effects. LA, leaf area in cm^2 ; SLA, specific leaf area in $\text{m}^2.\text{kg}^{-1}$; LDMC, leaf dry matter content in $\text{mg}.\text{g}^{-1}$; Height, vegetative height before harvest in cm; RD, mean root diameter in mm; SRL, specific root length in $\text{m}.\text{g}^{-1}$; RTD, root tissue density in $\text{g}.\text{cm}^{-3}$; RBI, root branching intensity in $\text{tips}.\text{cm}^{-1}$; Root: shoot, root: shoot ratio.

Predictor	Nested term (compartments)	n	Fixed effect						Random effect LRT test			
			chisq test	Intercept	Slope	CI slope low	CI slope high	Slope test ≠ 0	ID genotype	Block	R ² marginal	R ² conditional
Trait value isolated treatment	All	138	0.002 ^{NS}	-0.59	0.0002	-0.01	0.01	0.96	10.66**	0.27 ^{NS}	0	0.29
	Wild			-0.46	-0.02	-0.04	-0.006	0.01				
	First domesticated	138	12.21*	-0.46	-0.006	-0.02	0.008	0.42	6.92**	0.13 ^{NS}	0.12	0.32
	Durum landrace			-0.46	-0.005	-0.02	0.005	0.33				
	Durum elite			-0.46	-0.006	-0.02	0.005	0.32				
LA	All	137	3.18 ^{NS}	-0.91	0.02	-0.003	0.04	0.08	8.10*	0.90 ^{NS}	0.02	0.28
	Wild			-0.84	0.008	-0.01	0.03	0.46				
	First domesticated	137	14.19**	-0.84	0.02	-0.003	0.04	0.11	4.23*	0.76 ^{NS}	0.13	0.30
	Durum landrace			-0.84	0.02	-0.004	0.04	0.12				
	Durum elite			-0.84	0.02	-0.005	0.04	0.12				
SLA	All	137	0.01 ^{NS}	-0.58	-0.0002	-0.003	0.003	0.92	9.67**	0.33 ^{NS}	0	0.29
	Wild			-0.48	-0.008	-0.013	-0.003	0.002				
	First domesticated	137	18.36**	-0.48	-0.001	-0.005	0.003	0.58	4.41*	0 ^{NS}	0.15	0.3
	Durum landrace			-0.48	-0.001	-0.004	0.001	0.39				
	Durum elite			-0.48	-0.001	-0.005	0.002	0.41				
Height	All	132	0.40 ^{NS}	-0.48	-0.0004	-0.001	0.0009	0.53	12.29***	1.55 ^{NS}	0.003	0.34
	Wild			-0.50	-0.0009	-0.002	0.0005	0.21				
	First domesticated	132	17.09**	-0.5	-0.0002	-0.001	0.001	0.79	4.46*	2.77 ^{NS}	0.15	0.35
	Durum landrace			-0.5	-0.0002	-0.001	0.001	0.81				
	Durum elite			-0.5	-0.0002	-0.001	0.001	0.79				
LDMC	All	137	0.18 ^{NS}	-0.52	-0.27	-1.91	1.31	0.74	10.04**	0.26 ^{NS}	0.001	0.28
	Wild			-0.56	-0.56	-2.19	0.97	0.49				
	First domesticated	137	10.87*	-0.56	0.14	-1.52	1.7	0.87	5.90*	0.25 ^{NS}	0.11	0.3
	Durum landrace			-0.56	0.12	-1.57	1.69	0.89				
	Durum elite			-0.56	0.02	-1.65	1.59	0.98				
RD	All	138	3.31 ^{NS}	-0.73	-0.001	-0.00009	0.003	0.07	10.25**	0.15 ^{NS}	0.02	0.29
	Wild			-0.68	-0.00004	-0.002	0.002	0.96				
	First domesticated	138	9.68*	-0.68	0.001	-0.0003	0.003	0.12	6.98**	0 ^{NS}	0.09	0.29
	Durum landrace			-0.68	0.001	-0.0005	0.003	0.18				
	Durum elite			-0.68	0.001	-0.0002	0.003	0.1				
SRL	All	137	2.19 ^{NS}	-0.40	-1.33	-3.12	0.56	0.14	14.44***	0.21 ^{NS}	0.02	0.36
	Wild			-0.44	-1.83	-3.61	0.19	0.05				
	First domesticated	137	9.42 ^{NS}	-0.44	-0.74	-2.71	1.51	0.48	9.84**	1.34 ^{NS}	0.1	0.37
	Durum landrace			-0.44	-0.80	-2.50	1.14	0.37				
	Durum elite			-0.44	-0.87	-2.73	1.23	0.38				
RTD	All	138	0.23 ^{NS}	-0.51	-0.06	-0.32	0.2	0.64	11.47***	0.46 ^{NS}	0	0.29
	Wild			-0.41	-0.26	-0.53	0.03	0.074				
	First domesticated	138	12.42*	-0.41	-0.10	-0.36	0.18	0.47	6.95**	0.55 ^{NS}	0.12	0.33
	Durum landrace			-0.41	-0.10	-0.35	0.16	0.44				
	Durum elite			-0.41	-0.12	-0.38	0.15	0.36				
RBI	All	138	0.04 ^{NS}	-0.57	-0.06	-0.71	0.57	0.84	10.99***	0.30 ^{NS}	0	0.28
	Wild			-0.59	-0.48	-1.14	0.18	0.17				
	First domesticated	138	10.63*	-0.59	-0.18	-0.47	0.83	0.59	6.5*	0 ^{NS}	0.1	0.3
	Durum landrace			-0.59	-0.34	-0.51	1.15	0.43				
	Durum elite			-0.59	-0.1	-0.56	0.73	0.77				
Root:shoot	All	138	0.04 ^{NS}	-0.57	-0.06	-0.71	0.57	0.84	10.99***	0.30 ^{NS}	0	0.28
	Wild			-0.59	-0.48	-1.14	0.18	0.17				
	First domesticated	138	10.63*	-0.59	-0.18	-0.47	0.83	0.59	6.5*	0 ^{NS}	0.1	0.3
	Durum landrace			-0.59	-0.34	-0.51	1.15	0.43				
	Durum elite			-0.59	-0.1	-0.56	0.73	0.77				

Table S3. Linear mixed model results presenting the effects of trait values of the focal plant in competition treatment on focal competitive response. “All” correspond to results of a linear mixed model where data of all the compartments were pooled. The lines containing the four domestication compartments correspond to the results of nested linear mixed models. Genotype identity nested in domestication compartments and block position correspond to random effects. LA, leaf area in cm^2 ; SLA, specific leaf area in $\text{m}^2.\text{kg}^{-1}$; LDMC, leaf dry matter content in $\text{mg}.\text{g}^{-1}$; Height, vegetative height before harvest in cm; RD, mean root diameter in mm; SRL, specific root length in $\text{m}.\text{g}^{-1}$; RTD, root tissue density in $\text{g}.\text{cm}^{-3}$; RBI, root branching intensity in $\text{tips}.\text{cm}^{-1}$; Root: shoot, root: shoot ratio.

Predictor	Nested term (compartments)	n	Fixed effect						Random effect LRT test			
			chisq test	Intercept	Slope	CI slope low	CI slope high	Slope test ≠ 0	ID genotype	Block	R ² marginal	R ² conditional
Trait value in competition treatment												
LA	All	137	38.00***	-0.86	0.03	0.017	0.035	< 0.001	9.46**	0.77 ^{NS}	0.27	0.47
	Wild			-0.92	0.04	0.02	0.05	< 0.001				
	First domesticated	137	44.70***	-0.92	0.04	0.03	0.05	< 0.001	8.26**	0.50 ^{NS}	0.29	0.46
	Durum landrace			-0.92	0.03	0.02	0.04	< 0.001				
	Durum elite			-0.92	0.03	0.02	0.04	< 0.001				
SLA	All	137	0.90 ^{NS}	-0.39	-0.01	-0.03	0.01	0.34	10.59**	0.29 ^{NS}	0.007	0.29
	Wild			-0.3	-0.02	-0.04	0.0009	0.07				
	First domesticated	137	10.92*	-0.3	-0.01	-0.03	0.008	0.26	5.80*	0.27 ^{NS}	0.1	0.29
	Durum landrace			-0.3	-0.01	-0.04	0.009	0.25				
	Durum elite			-0.3	-0.01	-0.04	0.009	0.24				
Height	All	137	23.97***	-0.86	0.007	0.004	0.009	< 0.001	8.07**	0.32 ^{NS}	0.2	0.4
	Wild			-0.92	0.008	0.003	0.01	0.004				
	First domesticated	137	29.51***	-0.92	0.01	0.006	0.01	< 0.001	7.07**	0.11 ^{NS}	0.23	0.41
	Durum landrace			-0.92	0.007	0.004	0.01	< 0.001				
	Durum elite			-0.92	0.008	0.004	0.01	< 0.001				
LDMC	All	133	0.47 ^{NS}	-0.72	-0.0005	-0.001	0.002	0.5	8.45**	0.94 ^{NS}	0.003	0.28
	Wild			-0.60	-0.0005	-0.002	0.001	0.63				
	First domesticated	133	10.96*	-0.6	0.0003	-0.001	0.002	0.73	5.24*	0.88 ^{NS}	0.11	0.31
	Durum landrace			-0.6	0.0002	-0.001	0.002	0.78				
	Durum elite			-0.6	0.0001	-0.001	0.002	0.87				
RD	All	137	2.81 ^{NS}	-0.32	-1.02	-2.26	0.18	0.1	8.05**	0.11 ^{NS}	0.02	0.26
	Wild			-0.48	-0.76	-2.0	0.42	0.22				
	First domesticated	137	10.42*	-0.48	-0.17	-1.53	1.13	0.8	6.01*	0.15 ^{NS}	0.1	0.29
	Durum landrace			-0.48	-0.29	-1.72	1.09	0.69				
	Durum elite			-0.48	-0.28	-1.72	1.10	0.7				
SRL	All	133	0.35 ^{NS}	-0.63	0.0005	-0.001	0.002	0.56	8.76**	0 ^{NS}	0	0.25
	Wild			-0.57	-0.002	-0.004	0.0006	0.17				
	First domesticated	133	8.75 ^{NS}	-0.57	0.0003	-0.001	0.002	0.74	6.3*	0 ^{NS}	0.09	0.29
	Durum landrace			-0.57	0.0003	-0.002	0.002	0.76				
	Durum elite			-0.57	0.00009	-0.002	0.002	0.98				
RTD	All	135	0.12 ^{NS}	-0.62	0.29	-1.35	1.95	0.73	10**	0.16 ^{NS}	0	0.28
	Wild			-0.68	-0.09	-1.71	1.60	0.92				
	First domesticated	135	9.65*	-0.68	1.13	-0.74	3.08	0.26	6.14*	0.11 ^{NS}	0.1	0.30
	Durum landrace			-0.68	0.96	-0.68	2.64	0.27				
	Durum elite			-0.68	0.88	-0.82	2.61	0.33				
RBI	All	136	0.09 ^{NS}	-0.54	-0.04	-0.27	0.2	0.77	10.76**	0.17 ^{NS}	0	0.28
	Wild			-0.52	-0.15	-0.39	0.09	0.23				
	First domesticated	136	10.54*	-0.52	-0.01	-0.26	0.23	0.91	6.59*	0.15 ^{NS}	0.1	0.31
	Durum landrace			-0.52	-0.01	-0.25	0.22	0.9				
	Durum elite			-0.52	-0.02	-0.25	0.21	0.87				
Root:shoot	All	137	6.69**	-0.48	-0.53	-0.94	-0.11	0.01	5.66*	0.35 ^{NS}	0.05	0.25
	Wild			-0.53	-0.52	-0.92	-0.13	0.01				
	First domesticated	137	11.13*	-0.53	0.02	-0.69	0.72	0.97	4.98*	0.30 ^{NS}	0.1	0.28
	Durum landrace			-0.53	-0.10	-0.76	0.54	0.76				
	Durum elite			-0.53	-0.24	-0.92	0.44	0.5				

Table S4. Linear mixed model results presenting the effects of trait values of the focal plant plasticity on focal competitive response. “All” correspond to results of a linear mixed model where data of all the compartments were pooled. The lines containing the four domestication compartments correspond to the results of nested linear mixed models. Genotype identity nested in domestication compartments and block position correspond to random effects. LA, leaf area in cm^2 ; SLA, specific leaf area in $\text{m}^2.\text{kg}^{-1}$; LDMC, leaf dry matter content in $\text{mg}.\text{g}^{-1}$; Height, vegetative height before harvest in cm; RD, mean root diameter in mm; SRL, specific root length in $\text{m}.\text{g}^{-1}$; RTD, root tissue density in $\text{g}.\text{cm}^{-3}$; RBI, root branching intensity in $\text{tips}.\text{cm}^{-1}$; Root: shoot, root: shoot ratio.

Predictor	Nested term (compartments)	n	Fixed effect						Random effect LRT test			
			chisq test	Intercept	Slope	CI slope low	CI slope high	Slope test ≠ 0	ID genotype	Block	R ² marginal	R ² conditional
Trait plasticity to competition	All	138	84.92***	-0.45	0.58	0.45	0.71	< 0.001	0.36 ^{NS}	0.14 ^{NS}	0.39	0.42
	Wild			-0.45	0.64	0.49	0.8	< 0.001				
	First domesticated			-0.45	0.53	0.28	0.77	< 0.001				
	Durum landrace	138	84.50***	-0.45	0.52	0.32	0.74	< 0.001	0.79 ^{NS}	0.24 ^{NS}	0.39	0.44
	Durum elite			-0.45	0.46	0.24	0.71	< 0.001				
SLA	All	138	9.87**	-0.52	-0.41	-0.68	-0.14	0.002	6.15*	1.19 ^{NS}	0.07	0.29
	Wild			-0.52	-0.87	-1.23	-0.49	< 0.001				
	First domesticated			-0.52	-0.46	-0.96	0.08	0.09				
	Durum landrace	138	21.65***	-0.52	-0.16	-0.55	0.23	0.43	3.95*	1.92 ^{NS}	0.16	0.33
	Durum elite			-0.52	-0.25	-0.62	0.13	0.2				
Height	All	137	29.97***	-0.6	0.19	0.12	0.26	< 0.001	13.9***	0.89 ^{NS}	0.17	0.44
	Wild			-0.61	0.14	0.07	0.21	< 0.001				
	First domesticated			-0.61	0.46	0.19	0.73	0.001				
	Durum landrace	137	50.65***	-0.61	0.61	0.36	0.85	< 0.001	16.18***	1.07 ^{NS}	0.24	0.51
	Durum elite			-0.61	0.28	-0.08	0.64	0.14				
LDMC	All	130	2.3 ^{NS}	-0.59	0.22	-0.08	0.51	0.13	9.76**	2.66 ^{NS}	0.02	0.32
	Wild			-0.60	0.40	-0.04	0.82	0.08				
	First domesticated			-0.6	-0.16	-0.93	0.57	0.67				
	Durum landrace	130	4.20 ^{NS}	-0.6	0.02	-0.58	0.62	0.95	8.9**	2.55 ^{NS}	0.03	0.32
	Durum elite			-0.6	-0.34	-1.10	0.40	0.38				
RD	All	137	1.05 ^{NS}	-0.57	-0.13	-0.39	0.12	0.31	9.48**	0.31 ^{NS}	0.007	0.27
	Wild			-0.57	-0.27	-0.67	0.13	0.17				
	First domesticated			-0.57	0.20	-0.26	0.65	0.39				
	Durum landrace	137	12.36*	-0.57	-0.56	-1.00	-0.09	0.02	8.89**	0.74 ^{NS}	0.08	0.34
	Durum elite			-0.57	0.65	-0.03	1.34	0.07				
SRL	All	134	0.40 ^{NS}	-0.59	-0.04	-0.18	0.09	0.53	10.23**	0.09 ^{NS}	0	0.27
	Wild			-0.59	0.04	-0.24	0.33	0.78				
	First domesticated			-0.59	-0.04	-0.29	0.21	0.75				
	Durum landrace	134	6.32 ^{NS}	-0.59	0.18	-0.12	0.46	0.23	8.75**	0.18 ^{NS}	0.04	0.32
	Durum elite			-0.59	-0.26	-0.50	-0.02	0.03				
RTD	All	135	2.70 ^{NS}	-0.59	0.16	-0.03	0.35	0.1	13.78***	0.74 ^{NS}	0.02	0.34
	Wild			-0.59	-0.04	-0.43	0.33	0.83				
	First domesticated			-0.59	-0.11	-0.56	0.32	0.61				
	Durum landrace	135	7.80 ^{NS}	-0.59	0.43	0.04	0.8	0.03	14.59***	0.47 ^{NS}	0.05	0.38
	Durum elite			-0.59	0.25	-0.06	0.57	0.11				
RBI	All	137	0.27 ^{NS}	-0.59	0.06	-0.18	0.31	0.6	11.60***	0.05 ^{NS}	0	0.29
	Wild			-0.59	-0.01	-0.51	0.47	0.96				
	First domesticated			-0.59	-0.28	-0.75	0.18	0.24				
	Durum landrace	137	4.35 ^{NS}	-0.59	0.16	-0.38	0.71	0.57	9.33**	0 ^{NS}	0.03	0.29
	Durum elite			-0.59	0.35	-0.07	0.77	0.11				
Root:shoot	All	138	6.72**	-0.59	-0.11	-0.20	-0.02	0.01	6.03*	0.8 ^{NS}	0.05	0.26
	Wild			-0.59	-0.10	-0.23	0.02	0.1				
	First domesticated			-0.59	0.003	-0.26	0.27	0.98				
	Durum landrace	138	7.43 ^{NS}	-0.59	-0.14	-0.31	0.03	0.11	6.66**	0.61 ^{NS}	0.05	0.28
	Durum elite			-0.59	-0.18	-0.46	0.09	0.2				

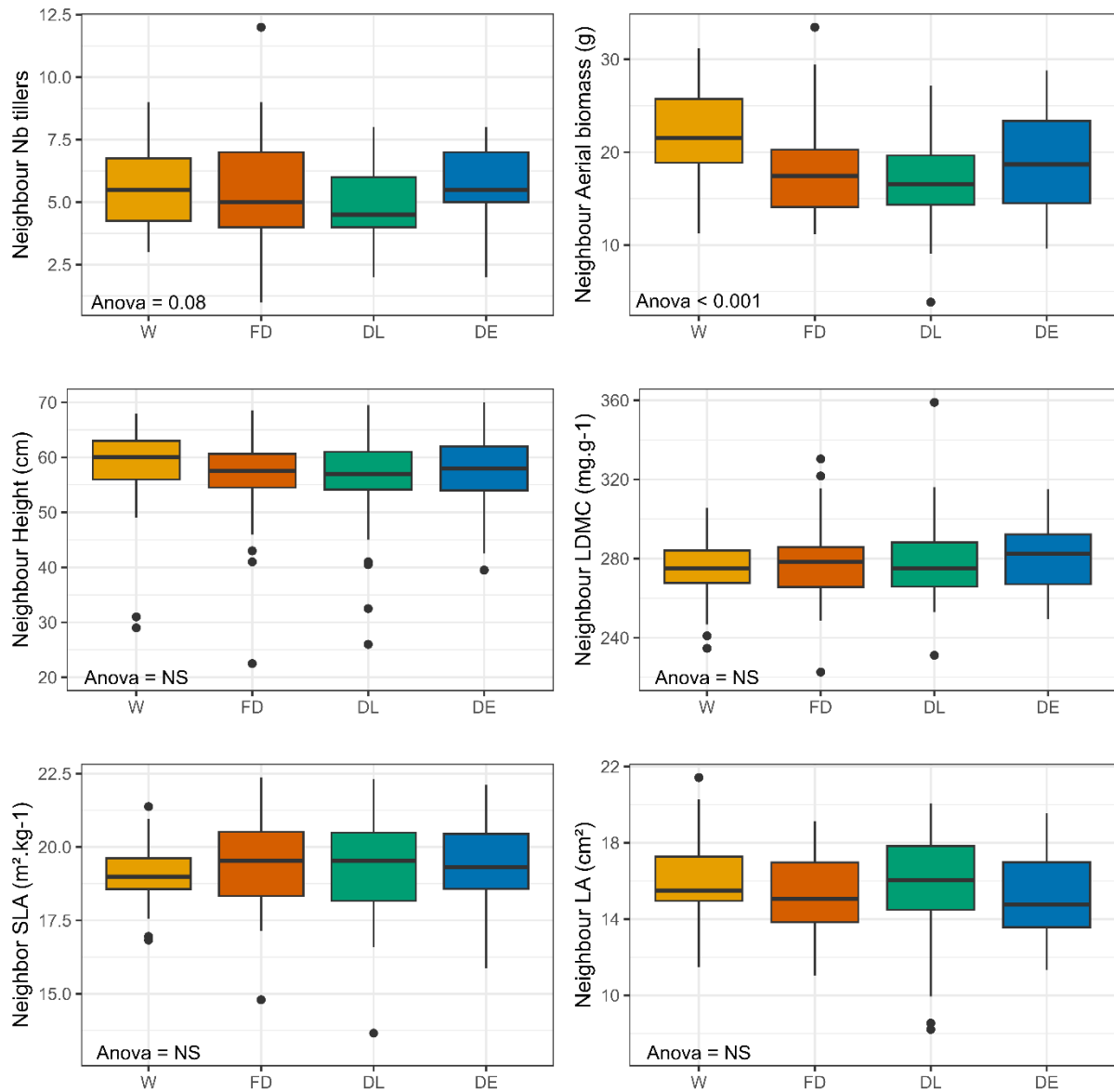


Figure S1. Neighbour traits variation depending on focal plant compartment. Nb tillers, number of tillers; Aerial biomass, vegetative biomass in g; Height, vegetative height before harvest in cm; LDMC, leaf dry matter content in mg.g⁻¹; SLA, specific leaf area in m².kg⁻¹; LA, leaf area in cm². Significance: ^{NS} P > 0.05; * P < 0.05, ** P < 0.01, *** P < 0.001.



Variété locale de blé dur

A. Rimlinger

CHAPITRE 3

*Experimental demonstration of allometric invariance of
plant response to density over the course of wheat
domestication*

Article en préparation

Lemoine, T., Fort, F, Vasseur, F, Gonzalez, E. A., Fréville, H., & Violle, C. (2023).
Experimental demonstration of allometric invariance of plant response to density over
the course of wheat domestication. *In Prep.*

I. Présentation générale

Dans le chapitre précédent, nous avons évalué la réponse à la compétition de 39 génotypes de blé dur appartenant à différents compartiments génétiques caractéristiques de son histoire évolutive. Nous avons montré des différences de réponse à la compétition entre les compartiments. Nous avons montré en particulier une meilleure performance des compartiments domestiqués du blé en réponse à la compétition. Mais qu'en est-il de sa réponse en peuplement mono-génotypique ?

L'objectif principal de ce dernier chapitre est, par une approche expérimentale, d'évaluer comment la réponse à la densité du blé dur et les contraintes allométriques sur la biomasse reproductive varient au cours de sa domestication et de la sélection moderne. Nous nous attendons à des changements dans la réponse à la densité au cours de la domestication et de la sélection moderne en raison de l'adaptation du blé à de fortes conditions de densité inhérentes aux systèmes cultivés (Khush, 2001). Nous nous attendons par ailleurs à des changements d'allocation entre la biomasse végétative et la biomasse reproductive dus à la sélection humaine pour la productivité en grain.

Pour tester ces hypothèses, nous semons les 39 génotypes issus de la série de domestication du blé dans des pots dans des conditions de densité de 1 à 10 plantes. Nous mesurons la biomasse végétative et reproductive à l'échelle du pot ainsi que plusieurs traits fonctionnels comme la date d'épiaison, la hauteur et le nombre de talles. Nous estimons également la biomasse végétative, la biomasse reproductive et le nombre de talles à l'échelle individuelle pour chaque génotype en divisant le total obtenu à l'échelle du pot par la densité du pot. Nous analysons les changements dans la réponse à la densité et dans l'allocation à la reproduction au cours de la domestication en utilisant une approche allométrique (relation log-log) (Deng *et al.*, 2008, 2012a,b; Li *et al.*, 2013; Qin *et al.*, 2013). En réponse à la densité, nous observons des ajustements phénotypiques à l'échelle individuelle. Les compartiments du blé réduisent leur nombre de talles et ont des dates d'épiaison plus précoce en réponse à l'augmentation de la densité de plantes. Dans cette étude, les compartiments du blé dur répondent de manière identique à l'augmentation de la densité. Nous montrons également une invariance dans les relations allométriques entre biomasse végétative et

reproductive au cours de l'histoire évolutive du blé dur. Ce chapitre met en évidence que les contraintes allométriques sont toujours présentes chez le blé dur malgré la sélection artificielle.

II. Abstract

- Selection under cultivation and breeding efforts to increase crop yield have led to major phenotypic changes, in particular changes in plant size. In ecology, trait-size relationships – so-called allometric relationships – have been repeatedly described as invariant across wild species, suggesting strong constraints on plant phenotypic evolution. By analogy, the action of artificial selection over the course of domestication and breeding might have been strongly constrained by plant allometry, but an experimental test is lacking.
- We used a collection of 39 genotypes representative of the four key stages (wild, first domesticated, landrace and elite) of the evolutionary history of durum wheat. We grew them in pots as monogenotypic culture, with increasing density from one to ten individuals. We measured biomass components and functional traits involved in plant competition (plant height, number of tillers and heading date) to evaluate fully the response of genotypes to density.
- In response to density, wheat genotypes drastically reduced their number of tillers and flowered earlier. However, we showed invariant biomass-based responses to density across the different stages of the evolutionary history of durum wheat. Furthermore, we highlighted that allometric relationships between vegetative biomass and reproductive biomass did not vary between wheat compartments despite major phenotypic changes.
- Our findings contribute to strengthening empirical knowledge on the phenotypic changes over the course of plant domestication. They highlight underexplored constraints on crop phenotypes, with direct implications for crop breeding.

III. Keywords

Crop environment, cultivated plant, density, plant size.

IV. Introduction

Numerous physiological, morphological and ecological traits vary as a function of size (West, 1999; Niklas, 2004), also known as allometric relationships (Huxley, 1924). Although plant phenotypic variation reflects plant adaptation to different environmental constraints (Grime, 1977; Westoby *et al.*, 2002; Diaz *et al.*, 2004), the parameters of trait-size relationships have been described as constants across taxa in the ecological literature (Enquist *et al.*, 1999; Brown *et al.*, 2004). Indeed, trait-size relationships are strongly constrained by biophysical and biomechanical laws. This idea was formalized in the Metabolic Scaling Theory (MST), a mechanistic theory that describes the first principles of plant allometric variations (West *et al.*, 1997, 1999; Enquist *et al.*, 1999). As an example, invariance of the parameters of the cross-species relationships between growth rate and plant dry biomass has been earlier documented (Niklas & Enquist, 2001). Moreover, a large body of theories highlights that plants' reproductive output is dependent on individual plant biomass (e.g., Klinkhamer *et al.*, 1992; Weiner *et al.*, 2009; Bonser & Aarssen, 2009), suggesting that producing a large amount of seeds depends mainly on the amount of biomass produced by a plant (Qin *et al.*, 2013). Those constraints at the plant level have implications at higher organizational levels. Indeed, the relationship between plant biomass and photosynthetic rate has been considered as constraints that could explain the well-documented decrease in plant biomass with population density (Deng *et al.*, 2008). Interestingly, Deng *et al.*, (2012b) suggested that crop response to density could be analyzed through a plant allometry lens, although the effect of artificial selection on plant allometry remains hardly explored (Deng *et al.*, 2008, 2012a,b; Li *et al.*, 2013; Qin *et al.*, 2013).

Invariance of plant allometry has recently been questioned since variation in allometric parameters has been observed among wild species (e.g., Poorter *et al.*, 2015) as well as within species (e.g., Vasseur *et al.*, 2018). This remaining variability suggests that natural selection could modulate allometric constraints (Glazier, 2022). While the action of natural selection is often difficult to evaluate in nature, the analysis of the effect of artificial selection – domestication and breeding in particular - on plant trait evolution is a promising way to test the robustness of allometric constraints (Milla *et al.*, 2015). Domestication has led to changes in morphology (Gioia *et al.*, 2015; Roucou *et al.*, 2018; Isaac *et al.*, 2021), reproduction (Fuller *et al.*, 2014) and biomass allocation patterns (Milla & Matesanz, 2017), leading to a general increase in the size of plant

organs, including leaves, reproductive parts and whole plants (Fuller *et al.*, 2014; Piperno *et al.*, 2015; Milla & Matesanz, 2017; Gómez-Fernández, 2023). This general increase in individual size probably led to greater levels of competition between cultivated plants, particularly for light capture (Milla, 2023). During the Green Revolution, crop breeders have reduced plant height through the introgression of semi-dwarfing genes, so as to increase crop resistance to lodging in response to fertilization (e.g., Niu *et al.*, 2022) and to limit competition for resources among plants (Donald, 1968; Anten & Vermeulen, 2016; Weiner, 2019). However, it is unclear whether morphological and allocation changes in response to domestication and breeding, modulated allometric constraints in crops.

Agricultural intensification has led to drastic increases in plant density over the last century (Fischer & Edmeades, 2010; Mansfield & Mumm, 2014). This has been made possible thanks to genetic improvement of resistance to lodging (e.g., short stature and root resistance), and to biotic stresses (e.g., disease and insect) and by increasing the level of available resources (high level of inputs), allowing crops to resist overcrowding and to maintain densely populated conditions (Duvick, 1986; Khush, 2001). Adaptation to cultivation systems led crop plants to overinvest in structures to quickly acquire resources and maximize their performance at the expense of group performance (Zhang *et al.*, 1999; Anten & Vermeulen, 2016). This was described as a *tragedy of the commons*, i.e., a situation in which competitive phenotypes in a population increase in frequency over generations, leading to resource depletion and a decrease in overall population performance (Hardin, 1968). Size reduction in crops has contributed to attenuate the expression of the tragedy of the commons in dense cultivated fields (Anten & Vermeulen, 2016) and has probably improved the ability of crops to perform under dense planting conditions. These improvements resulted in a substantial increase of yield components per unit of area such as grain yield for post-Green Revolution varieties (Hay, 1995; Royo *et al.*, 2021). The effect of domestication and artificial selection on size-density relationships, and how this relationship affected yield have been poorly tested so far. In this context, an allometry framework would be useful to explore changes in size-density relationships and traits that led to increased productivity during domestication and breeding (Deng *et al.*, 2012a,b).

Plants can express phenotypic plasticity under densely populated conditions in response to resource limitation. An expected response to density is the elongation of plant stem due to changes in light quality (i.e. shade response; Ballaré *et al.*, 1990; Dudley & Schmitt, 1996). In

grasses, a strong reduction of the number of tillers per plant has been observed at high density, due to a shortening of the tillering phase, reduced development of tillers under shaded conditions and high tiller regression at high density (Darwinkel, 1978; Evers *et al.*, 2006). Plants become lighter, grow in height rather than in width (Li *et al.*, 2013), suggesting some plasticity in allometric relationships (Weiner, 2004). However, these plastic responses have the disadvantage of reducing investment in reproductive effort in favor of a strategy of allocating resources to structures that increase the plants' competitive ability (Weiner, 2003). Breeding pressures to design a “weaker” cereal ideotype have standardized plant phenotype, which has probably limited plastic responses to plant competition in post-Green Revolution varieties (Kebrom & Brutnell, 2007; Weiner *et al.*, 2010; Colombo *et al.*, 2022; Beaugendre *et al.*, 2022).

Here, using 39 genotypes coming from four genetic compartments representative of different steps of the durum wheat domestication and breeding, we assessed how durum wheat phenotype differs between genetic compartments. Then, we explored, through an allometric framework, the effect of density on vegetative and reproductive biomass (Fig. 1, H1, H2) and tested for changes in allometric relationships between vegetative biomass and reproductive biomass across the different domestication stages (Fig. 1, H3). In addition, we tested whether plasticity to density of aboveground functional traits varied across domestication transect as a result of domestication and breeding. We expected a greater reproductive biomass at high density for post-Green Revolution varieties compared to wild progenitors due to better adaptation to high-density conditions and artificial selection on grain yield components (Fig.1, H1). We expected a greater increase in vegetative biomass (Fig.1, H2) and stronger response of aboveground traits for wild forms to density due to higher investment in structure involved in response to competition compared to post-Green Revolution varieties. Finally, we hypothesized that plant breeding may have shifted plant allocation towards reproductive effort (Fig.1, H3).

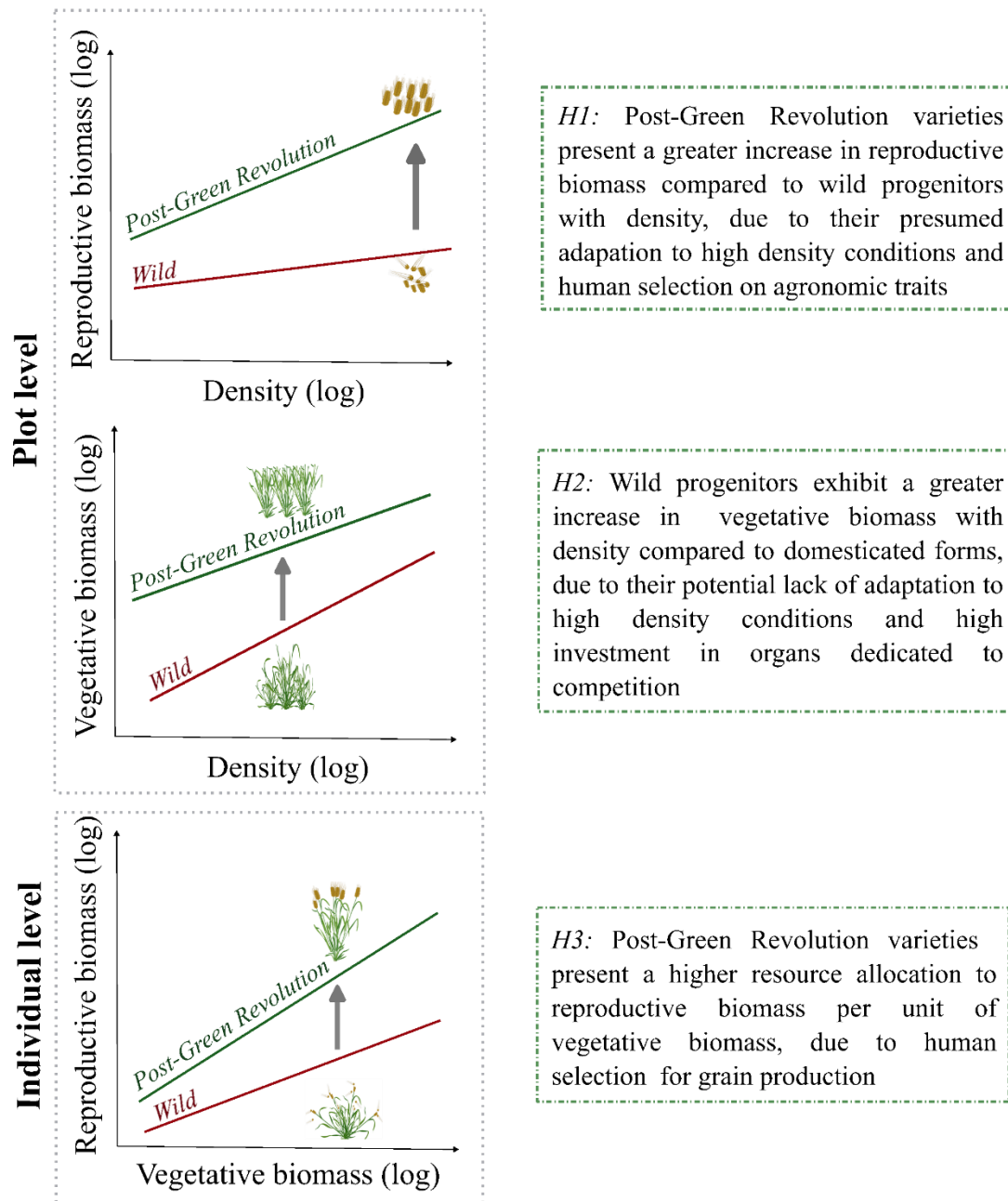


Figure 1. Conceptual diagram illustrating the expected changes, between wild wheat and its modern form, in vegetative and reproductive biomass in response to density and in allocation patterns between vegetative and reproductive biomass (reproductive effort). The harvest index, or reproductive effort in the ecological literature (Weiner *et al.*, 2009), corresponds to the fraction of biomass allocated to reproduction (Vega, 2000; Gaudio *et al.*, 2021). Wild correspond to crops wild progenitors. Post-Green revolution correspond to modern varieties shaped by genetic improvement during the Green Revolution.

V. Material and Methods

Plant material

We used 39 accessions from the domestication and breeding history of the tetraploid wheat *Triticum turgidum*: 10 accessions of the wild progenitor, the wild emmer, *T. turgidum* ssp. *dicoccoides* (W), 10 accessions of the first domesticated emmer *T. turgidum* ssp. *dicoccum* (FD), 10 landraces accessions of durum wheat *T. turgidum* ssp. *durum* belonging to the pre-Green Revolution period (DL), and 9 elite accessions of durum wheat registered in Europe after the Green Revolution (DE). Accessions were originally gathered from different international seed collections (Tab. S1) and further multiplied by selfing by UMR AGAP Institute, Montpellier, France.

Experimental design

We set up the experiment under outdoor conditions on the CEFÉ experimental field (France, 43°63'87''N, 3°86'26''E), from January to July 2022 (minimal temperature = -3.3°C and maximal temperature = 39.7°C). We performed a randomized block design using three blocks. The thirty-nine genotypes were grown in monogenotypic culture, from one to ten individuals per pot (i.e., 19 to 190 plants/m²). Each density modality was replicated three times (one replicate per block). Germination and bird attack issues occurred at the beginning of the experiment, leading to the loss of 111 pots out of 1170.

Genotypes were sown in 10-L plastic pots (26 cm diameter; 22 cm depth). We used local soil from the experimental field, composed of a sandy clay-limestone (132 g/kg of sand (0.05 to 0.2 mm), 120 g/kg of silt (0.002 to 0.02) and 179 g/kg of clay; 75 g/kg of CaCO₃; 37.9 g/kg of organic carbon; 1.83 g/kg of total N; 0.0787 g/kg of P; pH 7.8). It was fertilized with P and K fertilizer (0.64 g per pot in total of each fertilizer; P₂O₅ and K₂O) and ammonium nitrate (1.69g per pot in total). Pots were positioned on a tarpaulin on the ground and were interspaced (~30cm) to limit inter-pot competition for light. They were watered with tap water two to four times a week depending on rainfalls to avoid water excess and deficit. Plants were treated once for *Septoria tritici* blotch and aphids, respectively, with Bordeaux mixture (mixture of copper (II) sulphate (CuSO₄) and quicklime (CaO)) and rapeseed oil. Weeds were removed by hand throughout the duration of the experiment.

Aboveground trait and biomass measurements

At the end of the tillering stage, we counted the total number of tillers per pot. We measured plant vegetative height (cm; plant height), corresponding to the height between the soil and the highest leaf in the pot. We recorded heading date as the date at which spikes were visible for 50% of the plants in a pot. Heading dates were converted in growing degree days by summing the daily average temperatures since sowing using a 0°C base temperature. Meteorological data were obtained from the weather station of the experimental field at CEFÉ.

Genotypes were harvested from 14th of June to the 1st of July to allow plants to reach their maturity state. Additionally, the reproductive part of the wild genotypes was harvested daily due to their shattering spikes. Vegetative (leaves and stems) and reproductive (spikes with grains) biomasses were harvested separately, dried at 60° at least 72h and weighted. We calculated the reproductive effort as the ratio of spike biomass divided by the sum of vegetative biomass and spike biomass measured at pot level. We divided vegetative biomass, reproductive biomass and number of tillers measured at pot level by the density of plants in the pot to obtain individual measurements.

Data analyses

Before the analysis, we computed mean trait values per genotype at the pot level for each density modality. To explore changes in durum wheat phenotype during domestication and breeding, we first assessed the variation of aboveground trait values among domestication stages from pots where plants were grown alone. To do so, we performed a linear model (*lm* function), where domestication compartments (wild, first domesticated, durum landrace, durum elite) were considered as a fixed effect. We used multiple comparison tests (Tukey method, *lsmeans* function and package) to test for differences between domestication stages for each variable. Response variables were log transformed when necessary to meet normality assumptions.

We then analysed allometric relationships per domestication stage, according to the “allometric equation” (Huxley, 1924):

$$Y=\alpha M^{\beta} \tag{Eqn 1}$$

which is usually analysed as

$$\log_{10}(Y) = \log_{10}(\alpha) + \beta \log_{10}(M) \quad (\text{Eqn 2})$$

where α is the “allometric constant” corresponding to the y-intercept. The “scaling exponent” β is the slope of the relationship after log-transformation. It describes whether plant traits (Y) change proportionally (i.e., isometrically, $\beta = 1$) or allometrically (i.e., nonlinearly, $\beta \neq 1$), with M corresponding in the study to density (see Deng *et al.*, 2012a) or plant biomass (see Enquist *et al.*, 1999). To fit allometric relationships, two regression methods existed in the literature: Ordinary least squares (OLS) or Standardized Major Axis (SMA) regression. They differ in the assumptions concerning measurement error and lead to different slope estimates (Kilmer & Rodríguez, 2017). Unlike OLS, SMA is a symmetric regression that assumes measurement errors and residual errors on both axes, and not just the measurement error associated with the variable Y.

To test for changes in allometric relationships between individual reproductive biomass (Y in Eqn 2) and individual vegetative biomass (M in Eqn 2) between domestication compartments, we performed a standardized major axis (SMA, *smatr* package) regression, to consider measurement errors and residual errors on both axes. This enabled us to determine “scaling exponents” (slope) and “allometric constants” (intercept) for the relationship (log-log) between individual reproductive biomass (g) and individual vegetative biomass (g) for each compartment.

Secondly, we explored, through an allometric framework (Deng *et al.*, 2012a,b), the effect of density (M in Eqn 2) on vegetative and reproductive biomass (Y in Eqn 2). To do this, we performed this time, linear models (*lm()* function, Ordinary Least Squares regression, no measurement errors associated with density), between total reproductive biomass (g) and density of plant per m² and between total vegetative biomass (g) and density of plant per m², with an interaction term between plant density per m² and domestication stages (wild, first domesticated, durum landrace, durum elite).

Lastly, we assessed biomass (reproductive and vegetative biomass and reproductive effort) and aboveground traits (height, tiller numbers, heading date) response of plant individuals to density per domestication stages. We used linear models (*lm()* function), where the interaction of plant density per m² and domestication stages was considered as a fixed effect. Reproductive biomass, vegetative biomass, number of tillers and plant density, were log transformed to determine

allometric parameters. Pairwise comparisons of slopes between levels of domestication stages (adjusted p-value) were assessed using the *emtrends* function from the package *emmeans*.

VI. Results

Aboveground trait variation

Biomass components in isolated conditions changed significantly over the course of domestication and breeding (Fig. 2a, b). Genotypes from the wild compartment had the lowest vegetative and reproductive biomass, significantly lower than those of the first domesticated genotypes and landraces (Fig. 2a, b). The domesticated forms produced almost the same amount of reproductive biomass ($\mu\text{FD} = 16.8 \pm 1.2\text{g}$, $\mu\text{DL} = 17.7 \pm 1.2\text{g}$, $\mu\text{DE} = 15.8 \pm 1.3\text{g}$; Fig. 2a). Wild progenitors, landrace and elite compartments produced significantly less vegetative biomass than the first domesticated form ($p \leq 0.001$; Fig. 2b). Additionally, the ratio of the reproductive biomass on total biomass did not vary significantly over the course of domestication and breeding (Fig. 2c).

Aboveground traits significantly changed among durum wheat compartments (Fig. 2d, e, f). Plant height increased from wild forms to landraces, with first domesticated genotypes and landraces being significantly taller than wild genotypes (Fig. 2d). Plant height decreased between landraces and elite genotypes but not significantly ($p > 0.05$; Fig. 2d). Genotypes from the first domesticated form had the largest number of tillers, significantly larger than those of the landraces and elite genotypes ($p < 0.05$; Fig. 2e). First domesticated genotypes had a later heading date compared to the other three compartments (Fig. 2f).

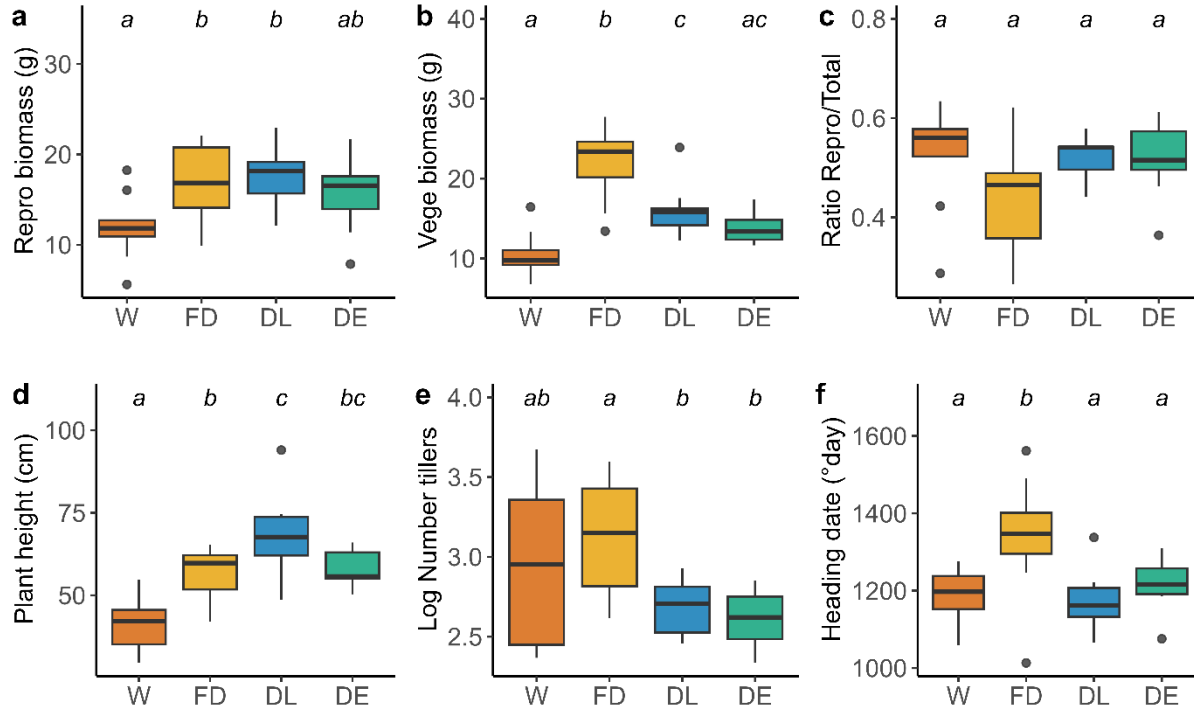


Figure 2. Variation of plant biomass components (a to c) and aboveground traits (d to f) of genotypes grown alone among the four stages of durum wheat domestication and breeding. a) Repro biomass: reproductive biomass in g; b) Vege biomass: vegetative biomass in g; c) Ratio Repro/Total: reproductive biomass divided by total biomass; d) Plant height: plant vegetative height in cm; e) Log Number of tillers; f) Heading date: heading date in growing degree day. Letters show significant mean differences between compartments. W, Wild; FD, First domesticated; DL, Durum landrace; DE, Durum elite.

Biomass response to density through a plant allometry lens

Reproductive and vegetative biomass at the pot level increased with increasing density for each compartment ($p < 0.001$; Fig. 3a, b; Tab. 1). The slope of the relationship between both reproductive and vegetative biomass and plant density did not significantly vary among compartments (Tab. 1).

At individual scale, vegetative biomass explained a significant and large part of reproductive biomass variation (Tab. 1; Fig. 3c). Reproductive biomass increased with vegetative biomass for all compartments (Fig. 3c). The slope of the relationship was significantly greater than one for the landrace and elite compartments (respectively, $p < 0.05$; $p < 0.01$; Tab. 1). No difference in slope between compartments was detected (Tab. 1). Moreover, genotypes from the first domesticated

stage had lower reproductive biomass than ones from the other stages for a given vegetative biomass (offset along the y-axis; Fig. 3c).

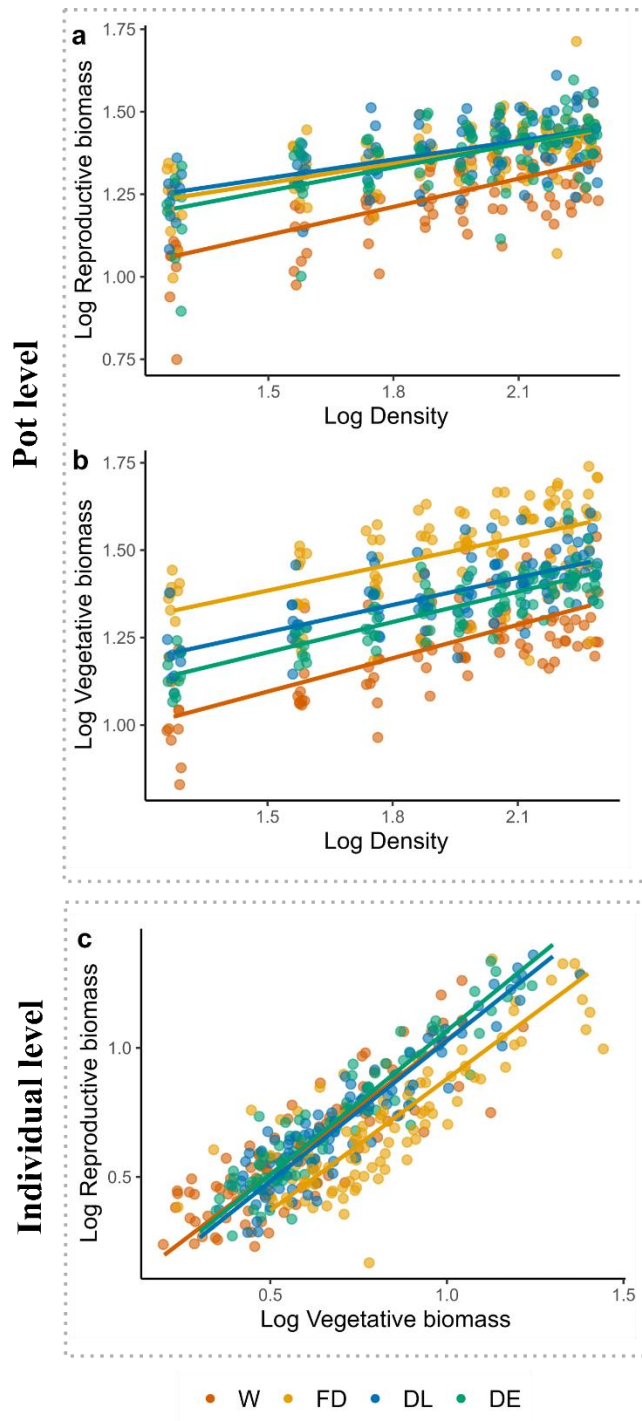


Figure 3. Allometric (log-log scale) relationships at the pot level between (a) Reproductive biomass and density; (b) Vegetative biomass and density, and at the individual level, between (c) Reproductive biomass and vegetative biomass, for the four durum wheat compartments. The coloured solid line shows the predicted relationship by the model. The coloured dots and lines correspond to the different compartments: Wild (Red), First domesticated (Orange), Durum landrace (Blue) and Durum elite (Green). Each dot represents the average value of the trait per genotype per density modality. We added random noise on the abscissa for density-biomass relationships (*position_jitter()* function) to avoid points overlapping.

Aboveground trait response to density

The individual response of reproductive and vegetative biomass to density did not vary between compartments (Fig. 4a, b; Tab. 1). All genotypes experienced a reduction in their individual reproductive and vegetative biomass in response to density (Fig. 4a, b). Moreover, landraces were the only ones for which the allocation to reproductive biomass per unit of vegetative biomass decreased significantly as density increased ($p < 0.05$; Fig. 4c; Tab. 1). There was no significant response of plant height to density for any compartment, but a trend was observed for wild genotypes which tended to increase their height in response to density ($p = 0.06$; Fig. 4d; Tab. 1). The individual number of tillers showed significant differential response to density between compartments (Fig. 4e; Tab. 1). First domesticated genotypes reduced their number of tillers more strongly in response to density compared to elite genotypes ($p < 0.01$; Tab. 1). Finally, wild, landrace and elite genotypes headed earlier in response to density (Fig. 4f; Tab. 1), with elite genotypes showing the strongest response ($\beta = -0.65$; Fig. 4f); yet, there was no significant difference in slopes with the other three compartments.

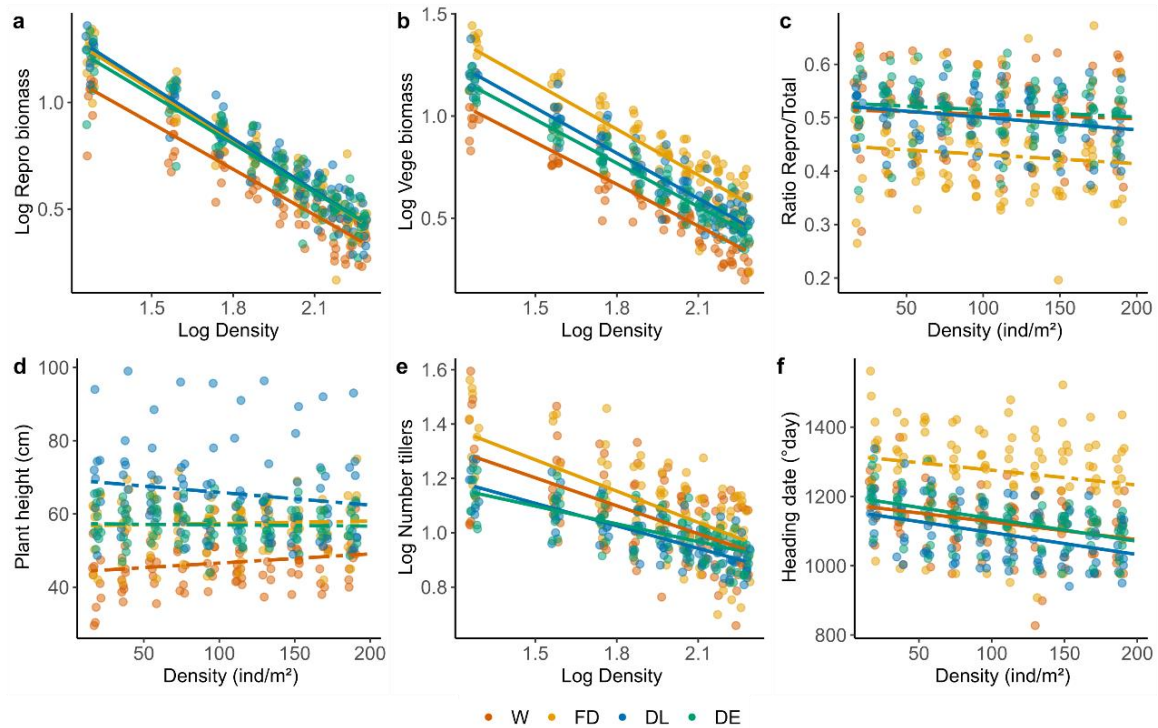


Figure 4. Variation of individual biomass components (a, b), reproductive to total biomass ratio (c) and aboveground traits (d to f) in response to density for wheat genotypes belonging to the four stages of durum wheat domestication and breeding. a) Log Repro biomass: reproductive biomass in g (log); b) Log Vege biomass: vegetative biomass in g (log); c) Ratio Repro/Total: ratio reproductive biomass/ Total biomass; d) Plant height: plant vegetative height in cm; e) Log Number of tillers; f) Heading date: heading date in growing degree day. Solid lines show significant relationships while dash lines show non-significant relationships. The coloured dots and lines correspond to the different compartments: Wild (Red), First domesticated (Orange), Durum landrace (Blue) and Durum elite (Green). Each dot represents the average value of the trait per genotype per density modality. We added random noise on the abscissa (*position_jitter()* function) to avoid point overlapping.

Table 1 Estimated coefficients of allometric relationships, and of relationships between traits and density per compartment at the pot (white colour) and individual level (grey colour). Confidence intervals are provided for intercept and slope coefficients. Different letters show significant slope differences between compartments. Between-group comparisons are not shown for response traits significantly associated with density. Adjusted coefficient of determination R² is given. Significance: ^{NS} P > 0.05; . P ~ 0.05; * P < 0.05, ** P < 0.01, *** P < 0.001.

Explanatory variable	Response variable	Domestic. stage	Intercept	Slope	Int_low CI	Int_high hCI	Slope_lowCI	Slope_highCI	R ²	Test slope group
Individual vegetative biomass	Individual reproductive biomass	W	-0.01	1.04	-0.08	0.06	0.93	1.16	0.71***	a
		FD	-0.14	1.02	-0.24	-0.04	0.91	1.14	0.68***	a
		DL	-0.06	1.09	-0.12	-0.004	1.02	1.17	0.88***	a
		DE	-0.05	1.1	-0.11	0.01	1.03	1.2	0.87***	a
Density	Pot reproductive biomass	W	0.7	0.28	0.59	0.82	0.22	0.35	0.45***	a
		FD	0.98	0.2	0.87	1.09	0.14	0.26	0.34***	a
		DL	1.02	0.19	0.91	1.12	0.14	0.24	0.34***	a
		DE	0.9	0.24	0.78	1.02	0.18	0.3	0.39***	a
	Pot vegetative biomass	W	0.62	0.32	0.49	0.75	0.25	0.38	0.48***	a
		FD	1	0.25	0.86	1.15	0.18	0.33	0.32***	a
		DL	0.88	0.26	0.78	0.97	0.21	0.31	0.51***	a
		DE	0.77	0.29	0.7	0.85	0.25	0.33	0.71***	a
Density	Individual reproductive biomass	W	1.97	-0.72	1.85	2.1	-0.78	-0.65	0.84***	a
		FD	2.26	-0.8	2.15	2.37	-0.85	-0.74	0.89***	a
		DL	2.29	-0.81	2.19	2.39	-0.86	-0.76	0.91***	a
		DE	2.18	-0.76	2.06	2.3	-0.82	-0.7	0.87***	a
	Individual vegetative biomass	W	1.89	-0.68	1.76	2.02	-0.75	-0.61	0.81***	a
		FD	2.28	-0.75	2.14	2.42	-0.82	-0.67	0.81***	a
		DL	2.15	-0.74	2.05	2.25	-0.79	0.69	0.90***	a
		DE	2.05	-0.71	1.97	2.12	-0.75	-0.67	0.94***	a
	Individual reproductive/ Total biomass	W	0.52	-0.00009	0.48	0.55	-0.0004	0.0002	0 ^{NS}	
		FD	0.45	-0.0002	0.41	0.48	-0.0005	0.0001	0 ^{NS}	
		DL	0.52	-0.0002	0.5	0.54	-0.0004	-0.0001	0.05*	
		DE	0.53	-0.0001	0.5	0.52	-0.0003	-0.0001	0 ^{NS}	
	Individual plant height	W	44.08	0.03	41.08	47.08	-0.001	0.05	0.03.	
		FD	56.74	0.01	53.77	59.7	-0.02	0.03	0 ^{NS}	
		DL	69.36	-0.03	64.14	74.58	-0.08	0.01	0.01 ^{NS}	
		DE	57.34	-0.003	55.05	59.63	-0.02	0.02	0 ^{NS}	
	Individual tillers number	W	1.72	-0.34	1.53	1.9	-0.44	-0.25	0.35***	ab
		FD	1.85	-0.38	1.68	2	-0.47	-0.3	0.45***	a
		DL	1.52	-0.28	1.44	1.6	-0.32	-0.23	0.64***	ab
		DE	1.42	-0.22	1.33	1.52	-0.26	-0.17	0.48***	b
Individual heading date	W	1178	-0.51	1143	1213	-0.82	-0.21	0.09**	a	
	FD	1319	-0.43	1261	1377	-0.95	0.66	0.02 ^{NS}		
	DL	1159	-0.63	1126	1191	-0.91	-0.36	0.16***	a	
	DE	1201	-0.65	1174	1228	-0.88	-0.42	0.25***	a	

VII. Discussion

Using a domestication series in durum wheat, we showed that the response to density of reproductive and vegetative biomass was surprisingly invariant throughout the history of wheat domestication and breeding. We also did not detect allometric changes in reproductive biomass despite the action of human selection to improve crop yield. We showed that plant functional traits changed between compartments, and all traits except plant height responded plastically to density, which could explain invariant responses modulated by phenotypic adjustments. As such, despite phenotypic variation between compartments, plant performance is primarily constrained by allometric laws.

We found that first domesticated forms and landraces produced higher reproductive and vegetative biomass than wild forms, suggesting that selective pressures during domestication led to larger and more productive plants. Increase in size of harvested organs in crops is a common outcome of plant domestication (Harlan *et al.*, 1973; Purugganan & Fuller, 2009; Fuller *et al.*, 2014). Moreover, Milla & Matesanz, (2017) showed in six crop species that domestication led to larger leaves allowing better light capture per individual and may have led to bigger plants due to whole-plant enlargement through the organ-to-organism allometry scaling. Increase in plant biomass could also be related to an increase in plant height in response to competitive conditions in agrosystems (Milla *et al.*, 2014; Milla & Matesanz, 2017; Milla, 2023). In particular, we found that landraces and first domesticated forms were taller than wild genotypes. We also detected a shift in tiller numbers between the first domesticated forms and landraces, with the latter having fewer tillers. Cultivated conditions have therefore led plants to invest in support structures by increasing their height rather than their width, in order to increase light acquisition in a dense stand and improve their individual performance (Weiner, 2004; Milla, 2023). As expected, breeding during the Green Revolution led to a reduction in the branching and stature of elite genotypes compared with landraces (lower tillers number, lower plant height; Donald, 1968; Coyne, 1980; Niu *et al.*, 2022). Despite phenotypic changes during domestication and breeding, we did not detect changes in the ratio of reproductive biomass to total biomass while reproductive effort experienced a substantial increase in the late 20th century (Hay, 1995; Gold, 1999). Yet, over the last century, considerable efforts have been made to improve cereal grain yields, both through genetic

improvements of cultivars and through changes in cultivation practices by increasing fertilization or density (Duvick, 1986; Austin *et al.*, 1989; Peltonen-Sainio & Karjalainen, 1991; Fischer & Edmeades, 2010).

In contrast to our hypotheses (Figure 1), we did not detect any differential response to density of biomass components over the course of wheat domestication and breeding. Sowing density has increased significantly in modern agriculture compared to traditional farming (Fischer & Edmeades, 2010). We might thus have expected selection under cultivation at high density to have contributed to adaptations in crop species to perform at high density (Postma *et al.*, 2021). What is most surprising is that breeding effort to decrease lodging and intraspecific competition (Donald, 1968) does not lead to a smaller increase in vegetative biomass with density in post-Green Revolution compartment compared to other compartments. Invariance of biomass response to density between compartments could be explained by similar constraints on plant growth. Indeed, scaling relationships between metabolic rate, body size and population have been described as universal across taxa (Brown *et al.*, 2004). The constraints imposed on individual biomass by high density conditions will then limit other functions as reproduction (Weiner *et al.*, 2009). Another explanation could be linked to constraints imposed by experiments in pots. Indeed, the substrate volume strongly constraints the size of the root system, which can have a strong effect on shoot growth (Poorter *et al.*, 2012a; Freschet *et al.*, 2021). As such, we strongly encourage future research to investigate allometric relationships in crops under field conditions.

We highlighted tight relationships between vegetative biomass and reproductive biomass for all domestication stages, suggesting that most of the variation of reproductive biomass was explained by variation of vegetative biomass reached by the plants. Allocation patterns, particularly allocation to reproductive structures, have already been shown to be size dependent (Weiner, 2004; Weiner *et al.*, 2009; Qin *et al.*, 2013). Indeed, biomass accumulation and partitioning during growth play a central role in fueling all plant structures (e.g., structural tissues, vegetative organs, reproductive structure) (Poorter & Sack, 2012; Poorter *et al.*, 2012b). Modern selection has modulated resource allocation patterns and morphology in crop species to promote resource allocation to grain yield in cereals (Evans, 1996; Milla & Matesanz, 2017). Surprisingly though, allometric slopes did not vary between compartments. Allometry represents a strong developmental constraint on phenotypic evolution (Pélabon *et al.*, 2014). Our result suggests that allometric constraints are not easily breakable, even through the action of artificial selection (Egset *et al.*,

2012; Pélabon *et al.*, 2014; Voje *et al.*, 2014). Egset *et al.*, (2012) through an artificial selection experiment on male guppies, showed that it seems actually easier to modulate allometric intercepts than allometric slopes because directional selection acts directly on the value of the underlying traits. This could explain why we mainly found an effect of domestication and breeding on phenotypic trait values rather on covariation between biomass traits. Yet, we found that landraces and elite genotypes had an allometric slope significantly greater than one, meaning that genotypes with higher vegetative biomass have relatively higher reproductive biomass. This positive allometry can be interpreted as a possible effect of directional selection on agronomic traits of interest. The assessment of allometric relationships in crops merits further research to understand how to overcome these constraints and increase allocation to reproduction (Denison, 2015).

All genotypes underwent a reduction in their vegetative biomass in response to density whatever the domestication stage. Decrease in individual vegetative biomass is characteristic of strong intraspecific competition, due to the limitation of light and nutrient resources with increasing density (Bleasdale, 1966; Weiner & Freckleton, 2010). These results suggest that the different wheat compartments respond in the same way to the reduction in resource availability when they are in competition with conspecifics. We also demonstrated a reduction in reproductive biomass with density, probably due to a retroactive effect of limiting plant growth with competition, and therefore fewer resources to allocate to other functions (Weiner, 2004). The ratio of reproductive biomass to total biomass decreased in response to density only for landraces. Qin *et al.* (2013) found that this ratio is size dependent and varies differently in response to density for different wheat varieties.

Despite invariance of biomass response to density between compartments, functional traits of genotypes changed plastically with density and these changes are compartment-dependent. In particular, we highlighted a reduction of tiller number and earlier heading date in response to density. Such plastic response reflects classical plant response to competition for nutrient and light (Weiner & Thomas, 1986; Weiner, 2004; Beaugendre *et al.*, 2022). Genotypes from the first domesticated form reduced more strongly their tiller number with density compared to elite forms. This could result from the fact that tillering is a major trait for cereal yield, targeted by breeding, which likely reduced trait variation and constrained tiller response (Kebrom *et al.*, 2012). We therefore observed a phenotypic adjustment of plant shape to respond to density, i.e., plants becoming lighter and less bulky as already reported in other studies (Li *et al.*, 2013).

Our results call for the use of an allometric framework to consider size constraints into the trait-to-crop performance mapping. Plant density response has been hardly analyzed through a plant allometry lens, despite the great potential of this approach for optimizing crop density and yield (Deng *et al.*, 2012a; Li *et al.*, 2013; Qin *et al.*, 2013). Invariance of the response to density and allometric constraints despite artificial selection demonstrate that crop phenotype remains constrained by multiple biomechanical or ecophysiological laws that severely limit crop improvement. Future fruitful interactions between disciplines will enable us to better identify the genetic drivers behind allometric constraints on plant phenotype, and perhaps overcome them.

VIII. Acknowledgements

We thank the TE platform team of the LabEx CeMEB for providing all the facilities and technical support. Experimental work was supported by the Agence Nationale de la Recherche (ANR) project “Selecting for cooperative crops to develop sustainable agriculture” (SCOOP, grant no. ANR-19-CE32-0011).

IX. Author contributions

CV, HF, FF, and TL, planned and designed the research. EG, AR and TL performed the experiment. TL analysed the data. TL, CV, FF and HF wrote the first version of the manuscript, with inputs from FV. All authors read and approved the final manuscript.

X. Data availability

The data to reproduce all analyses of this paper can be accessed at [to be completed upon final acceptance].

XI. References

- Anten NPR, Vermeulen PJ. 2016.** Tragedies and Crops: Understanding Natural Selection To Improve Cropping Systems. *Trends in Ecology & Evolution* **31**: 429–439.
- Austin RB, Ford MA, Morgan CL. 1989.** Genetic improvement in the yield of winter wheat: a further evaluation. *The Journal of Agricultural Science* **112**: 295–301.
- Ballaré CL, Scopel AL, Sánchez RA. 1990.** Far-Red Radiation Reflected from Adjacent Leaves: An Early Signal of Competition in Plant Canopies. *Science* **247**: 329–332.
- Beaugendre A, Mingeot D, Visser M. 2022.** Complex plant interactions in heterogeneous material require the ecological rethinking of sowing density recommendations for bread wheat. A review. *Agronomy for Sustainable Development* **42**: 9.
- Bleasdale JKA. 1966.** Plant growth and crop yield: The fourth Barnes Memorial Lecture. *Annals of Applied Biology* **57**: 173–182.
- Bonser SP, Aarssen LW. 2009.** Interpreting reproductive allometry: Individual strategies of allocation explain size-dependent reproduction in plant populations. *Perspectives in Plant Ecology, Evolution and Systematics* **11**: 31–40.
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004.** Toward a Metabolic Theory of Ecology. *Ecology* **85**: 1771–1789.
- Colombo M, Montazeaud G, Viader V, Ecartot M, Prospero J-M, David J, Fort F, Violle C, Fréville H. 2022.** A genome-wide analysis suggests pleiotropic effects of Green Revolution genes on shade avoidance in wheat. *Evolutionary Applications* **15**: 1594–1604.
- Coyne DP. 1980.** Modification of Plant Architecture and Crop Yield by Breeding¹. *HortScience* **15**: 244–247.
- Cunniff J, Wilkinson S, Charles M, Jones G, Rees M, Osborne CP. 2014.** Functional Traits Differ between Cereal Crop Progenitors and Other Wild Grasses Gathered in the Neolithic Fertile Crescent. *PLOS ONE* **9**: e87586.
- Darwinkel A. 1978.** Patterns of tillering and grain production of winter wheat at a wide range of plant densities. *Netherlands Journal of Agricultural Science* **26**: 383–398.
- Deng J-M, Li T, Wang G-X, Liu J, Yu Z-L, Zhao C-M, Ji M-F, Zhang Q, Liu J. 2008.** Trade-Offs between the Metabolic Rate and Population Density of Plants. *PLOS ONE* **3**: e1799.
- Deng J, Ran J, Wang Z, Fan Z, Wang G, Ji M, Liu J, Wang Y, Liu J, Brown JH. 2012a.** Models and tests of optimal density and maximal yield for crop plants. *Proceedings of the National Academy of Sciences* **109**: 15823–15828.
- Deng J, Zuo W, Wang Z, Fan Z, Ji M, Wang G, Ran J, Zhao C, Liu J, Niklas KJ, et al. 2012b.** Insights into plant size-density relationships from models and agricultural crops. *Proceedings of the National Academy of Sciences* **109**: 8600–8605.

- Denison RF. 2015.** Evolutionary tradeoffs as opportunities to improve yield potential. *Field Crops Research* **182**: 3–8.
- Diaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, Montserrat-Martí G, Grime JP, Zarrinkamar F, Asri Y, et al. 2004.** The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science* **15**: 295–304.
- Donald CM. 1968.** The breeding of crop ideotypes. *Euphytica* **17**: 385–403.
- Dudley SA, Schmitt J. 1996.** Testing the Adaptive Plasticity Hypothesis: Density-Dependent Selection on Manipulated Stem Length in *Impatiens capensis*. *The American Naturalist* **147**: 445–465.
- Duvick DN. 1986.** Plant breeding: Past achievements and expectations for the future. *Economic Botany* **40**: 289–297.
- Egset CK, Hansen TF, Le Rouzic A, Bolstad GH, Rosenqvist G, Pélabon C. 2012.** Artificial selection on allometry: change in elevation but not slope. *Journal of Evolutionary Biology* **25**: 938–948.
- Enquist BJ, West GB, Charnov EL, Brown JH. 1999.** Allometric scaling of production and life-history variation in vascular plants. *Nature* **401**: 907–911.
- Evans LT. 1996.** *Crop Evolution, Adaptation and Yield*. Cambridge University Press.
- Evers JB, Vos J, Andrieu B, Struik PC. 2006.** Cessation of Tillering in Spring Wheat in Relation to Light Interception and Red : Far-red Ratio. *Annals of Botany* **97**: 649–658.
- Fischer RAT, Edmeades GO. 2010.** Breeding and Cereal Yield Progress. *Crop Science* **50**: S-85-S-98.
- Freschet GT, Pagès L, Iversen CM, Comas LH, Rewald B, Roumet C, Klimešová J, Zadworny M, Poorter H, Postma JA, et al. 2021.** A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. *New Phytologist* **232**: 973–1122.
- Fuller DQ, Denham T, Arroyo-Kalin M, Lucas L, Stevens CJ, Qin L, Allaby RG, Purugganan MD. 2014.** Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record. *Proceedings of the National Academy of Sciences* **111**: 6147–6152.
- Gaudio N, Violle C, Gendre X, Fort F, Mahmoud R, Pelzer E, Médiène S, Hauggaard-Nielsen H, Bedoussac L, Bonnet C, et al. 2021.** Interspecific interactions regulate plant reproductive allometry in cereal–legume intercropping systems. *Journal of Applied Ecology* **58**: 2579–2589.
- Gioia T, Nagel KA, Beleggia R, Fragasso M, Ficco DBM, Pieruschka R, De Vita P, Fiorani F, Papa R. 2015.** Impact of domestication on the phenotypic architecture of durum wheat under contrasting nitrogen fertilization. *Journal of Experimental Botany* **66**: 5519–5530.
- Glazier DS. 2022.** Variable metabolic scaling breaks the law: from ‘Newtonian’ to ‘Darwinian’ approaches. *Proceedings of the Royal Society B: Biological Sciences* **289**: 20221605.
- Gold MV. 1999.** *Sustainable Agriculture: Definitions and Terms*. National Agricultural Library.
- Gómez-Fernández A. 2023.** Plant size variation in crops: causes, mechanisms and consequences.

- Grime JP. 1977.** Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist* **111**: 1169–1194.
- Hardin G. 1968.** The Tragedy of the Commons. *Science* **162**: 1243–1248.
- Harlan JR. 1967.** A wild wheat harvest in Turkey. *Archaeology* **20**: 197–201.
- Harlan JR, de Wet JM, Price EG. 1973.** Comparative Evolution of Cereals. *Evolution* **27**: 311–325.
- Hay RKM. 1995.** Harvest index: a review of its use in plant breeding and crop physiology. *Annals of Applied Biology* **126**: 197–216.
- Huxley JS. 1924.** Constant Differential Growth-Ratios and their Significance. *Nature* **114**: 895–896.
- Isaac ME, Nimmo V, Gaudin ACM, Leptin A, Schmidt JE, Kallenbach CM, Martin A, Entz M, Carkner M, Rajcan I, et al. 2021.** Crop Domestication, Root Trait Syndromes, and Soil Nutrient Acquisition in Organic Agroecosystems: A Systematic Review. *Frontiers in Sustainable Food Systems* **5**: 716480.
- Jones G, Kluyver T, Preece C, Swarbrick J, Forster E, Wallace M, Charles M, Rees M, Osborne CP. 2021.** The origins of agriculture: Intentions and consequences. *Journal of Archaeological Science* **125**: 105290.
- Kebrom TH, Brutnell TP. 2007.** The molecular analysis of the shade avoidance syndrome in the grasses has begun. *Journal of Experimental Botany* **58**: 3079–3089.
- Kebrom TH, Chandler PM, Swain SM, King RW, Richards RA, Spielmeier W. 2012.** Inhibition of Tiller Bud Outgrowth in the tin Mutant of Wheat Is Associated with Precocious Internode Development. *Plant Physiology* **160**: 308–318.
- Khush GS. 2001.** Green revolution: the way forward. *Nature Reviews Genetics* **2**: 815–822.
- Kilmer JT, Rodríguez RL. 2017.** Ordinary least squares regression is indicated for studies of allometry. *Journal of Evolutionary Biology* **30**: 4–12.
- Klinkhamer PGL, Meelis E, de Jong TJ, Weiner J. 1992.** On the Analysis of Size-Dependent Reproductive Output in Plants. *Functional Ecology* **6**: 308–316.
- Ladizinsky G. 1975.** Collection of Wild Cereals in the Upper Jordan Valley. *Economic Botany* **29**: 264–267.
- Li L, Weiner J, Zhou D, Huang Y, Sheng L. 2013.** Initial density affects biomass–density and allometric relationships in self-thinning populations of *Fagopyrum esculentum*. *Journal of Ecology* **101**: 475–483.
- Lu S, Dong L, Fang C, Liu S, Kong L, Cheng Q, Chen L, Su T, Nan H, Zhang D, et al. 2020.** Stepwise selection on homeologous PRR genes controlling flowering and maturity during soybean domestication. *Nature Genetics* **52**: 428–436.
- Mansfield BD, Mumm RH. 2014.** Survey of Plant Density Tolerance in U.S. Maize Germplasm. *Crop Science* **54**: 157–173.

- Martín-Robles N, Morente-López J, Freschet GT, Poorter H, Roumet C, Milla R. 2019.** Root traits of herbaceous crops: Pre-adaptation to cultivation or evolution under domestication? *Functional Ecology* **33**: 273–285.
- Milla R. 2023.** Phenotypic evolution of agricultural crops. *Functional Ecology* **37**: 976–988.
- Milla R, Matesanz S. 2017.** Growing larger with domestication: a matter of physiology, morphology or allocation? *Plant Biology* **19**: 475–483.
- Milla R, Morente-López J, Alonso-Rodrigo JM, Martín-Robles N, Stuart Chapin F. 2014.** Shifts and disruptions in resource-use trait syndromes during the evolution of herbaceous crops. *Proceedings of the Royal Society B: Biological Sciences* **281**: 20141429.
- Milla, Osborne CP, Turcotte MM, Violle C. 2015.** Plant domestication through an ecological lens. *Trends in Ecology & Evolution* **30**: 463–469.
- Niklas KJ. 2004.** Plant allometry: is there a grand unifying theory? *Biological Reviews* **79**: 871–889.
- Niklas KJ, Enquist BJ. 2001.** Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proceedings of the National Academy of Sciences* **98**: 2922–2927.
- Niu Y, Chen T, Zhao C, Zhou M. 2022.** Lodging prevention in cereals: Morphological, biochemical, anatomical traits and their molecular mechanisms, management and breeding strategies. *Field Crops Research* **289**: 108733.
- Pélabon C, Firmat C, Bolstad GH, Voje KL, Houle D, Cassara J, Rouzic AL, Hansen TF. 2014.** Evolution of morphological allometry. *Annals of the New York Academy of Sciences* **1320**: 58–75.
- Peltonen-Sainio P, Karjalainen R. 1991.** Genetic Yield Improvement of Cereal Varieties in Northern Agriculture since 1920. *Acta Agriculturae Scandinavica* **41**: 267–273.
- Piperno DR, Holst I, Winter K, McMillan O. 2015.** Teosinte before domestication: Experimental study of growth and phenotypic variability in Late Pleistocene and early Holocene environments. *Quaternary International* **363**: 65–77.
- Poorter H, Bühler J, Van Dusschoten D, Climent J, Postma JA. 2012a.** Pot size matters: a meta-analysis of the effects of rooting volume on plant growth. *Functional Plant Biology* **39**: 839.
- Poorter H, Jagodzinski AM, Ruiz-Peinado R, Kuyah S, Luo Y, Oleksyn J, Usoltsev VA, Buckley TN, Reich PB, Sack L. 2015.** How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytologist* **208**: 736–749.
- Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012b.** Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* **193**: 30–50.
- Poorter H, Sack L. 2012.** Pitfalls and Possibilities in the Analysis of Biomass Allocation Patterns in Plants. *Frontiers in Plant Science* **3**: 259.
- Postma JA, Hecht VL, Hikosaka K, Nord EA, Pons TL, Poorter H. 2021.** Dividing the pie: A quantitative review on plant density responses. *Plant, Cell & Environment* **44**: 1072–1094.

- Preece C, Clamp NF, Warham G, Charles M, Rees M, Jones G, Osborne CP. 2018.** Cereal progenitors differ in stand harvest characteristics from related wild grasses. *Journal of Ecology* **106**: 1286–1297.
- Purugganan MD, Fuller DQ. 2009.** The nature of selection during plant domestication. *Nature* **457**: 843–848.
- Qin X, Weiner J, Qi L, Xiong Y, Li F. 2013.** Allometric analysis of the effects of density on reproductive allocation and Harvest Index in 6 varieties of wheat (*Triticum*). *Field Crops Research* **144**: 162–166.
- Roucou A, Violle C, Fort F, Roumet P, Ecartot M, Vile D. 2018.** Shifts in plant functional strategies over the course of wheat domestication. *Journal of Applied Ecology* **55**: 25–37.
- Royo C, Ammar K, Villegas D, Soriano JM. 2021.** Agronomic, Physiological and Genetic Changes Associated With Evolution, Migration and Modern Breeding in Durum Wheat. *Frontiers in Plant Science* **12**.
- Vasseur F, Exposito-Alonso M, Ayala-Garay OJ, Wang G, Enquist BJ, Vile D, Violle C, Weigel D. 2018.** Adaptive diversification of growth allometry in the plant *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences* **115**: 3416–3421.
- Vega C. 2000.** Reproductive Allometry in Soybean, Maize and Sunflower. *Annals of Botany* **85**: 461–468.
- Voje KL, Hansen TF, Egset CK, Bolstad GH, Pélabon C. 2014.** Allometric constraints and the evolution of allometry. *Evolution* **68**: 866–885.
- Weiner J. 2003.** Ecology – the science of agriculture in the 21st century. *The Journal of Agricultural Science* **141**: 371–377.
- Weiner J. 2004.** Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics* **6**: 207–215.
- Weiner J. 2019.** Looking in the Wrong Direction for Higher-Yielding Crop Genotypes. *Trends in Plant Science* **24**: 927–933.
- Weiner J, Andersen SB, Wille WK-M, Griepentrog HW, Olsen JM. 2010.** Evolutionary Agroecology: the potential for cooperative, high density, weed-suppressing cereals. *Evolutionary Applications* **3**: 473–479.
- Weiner J, Campbell LG, Pino J, Echarte L. 2009.** The allometry of reproduction within plant populations. *Journal of Ecology* **97**: 1220–1233.
- Weiner J, Freckleton RP. 2010.** Constant Final Yield. *Annual Review of Ecology, Evolution, and Systematics* **41**: 173–192.
- Weiner J, Thomas SC. 1986.** Size Variability and Competition in Plant Monocultures. *Oikos* **47**: 211–222.
- West GB. 1999.** The origin of universal scaling laws in biology. *Physica A: Statistical Mechanics and its Applications* **263**: 104–113.
- West GB, Brown JH, Enquist BJ. 1997.** A General Model for the Origin of Allometric Scaling Laws in Biology. *Science* **276**: 122–126.

West GB, Brown JH, Enquist BJ. 1999. A general model for the structure and allometry of plant vascular systems. *Nature* **400**: 664–667.

Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002. Plant Ecological Strategies: Some Leading Dimensions of Variation Between Species. *Annual Review of Ecology and Systematics* **33**: 125–159.

Zhang D-Y, Sun G-J, Jiang X-H. 1999. Donald's ideotype and growth redundancy: a game theoretical analysis. *Field Crops Research* **61**: 179–187.

SUPPLEMENTARY INFORMATION

*Experimental demonstration of allometric invariance of plant
response to density over the course of wheat domestication*

XII. Supporting Information

Table S1. List of accessions. Seeds were provided by INRAE UMR AGAP in Montpellier, France.

INRAE accession number	International accession number	Collection	Compartment
48	46499	Icarda	<i>dicoccoides</i>
50	46491	Icarda	<i>dicoccoides</i>
62	46309	Icarda	<i>dicoccoides</i>
63	46310	Icarda	<i>dicoccoides</i>
71	46453	Icarda	<i>dicoccoides</i>
73	46253	Icarda	<i>dicoccoides</i>
75	116179	Icarda	<i>dicoccoides</i>
83	466987	USDA	<i>dicoccoides</i>
85	467014	USDA	<i>dicoccoides</i>
90	352324	USDA	<i>dicoccoides</i>
116	45383	Icarda	<i>dicoccum</i>
128	45351	Icarda	<i>dicoccum</i>
130	45239	Icarda	<i>dicoccum</i>
137	45354	Icarda	<i>dicoccum</i>
139	45280	Icarda	<i>dicoccum</i>
143	45441	Icarda	<i>dicoccum</i>
157	352365	USDA	<i>dicoccum</i>
184	415152	USDA	<i>dicoccum</i>
202	319868	USDA	<i>dicoccum</i>
208	cwi17084	CIMMYT	<i>dicoccum</i>
250	edmore (495)	montpellier	<i>durum</i>
302	84866	Icarda	<i>durum</i>
312	97512	Icarda	<i>durum</i>
328	95920	Icarda	<i>durum</i>
344	82697	Icarda	<i>durum</i>
346	82702	Icarda	<i>durum</i>
349	82768	Icarda	<i>durum</i>
351	82726	Icarda	<i>durum</i>
354	82715	Icarda	<i>durum</i>
362	AGATHE	GEVES	<i>durum</i>
374	DURGAMM	GEVES	<i>durum</i>
380	NITA	GEVES	<i>durum</i>
382	ROMEO	GEVES	<i>durum</i>
395	PRIMADUR	GEVES	<i>durum</i>
405	ARBOIS	GEVES	<i>durum</i>
411	NEODUR	GEVES	<i>durum</i>
430	IXOS	GEVES	<i>durum</i>
437	DURENTAL	GEVES	<i>durum</i>
581	B6R	(maria)	<i>durum</i>



Variété élite de blé dur

A. Rimlinger

DISCUSSION

Il est encore impossible de passer par une porte spatio-temporelle et de se retrouver projeté des millénaires en arrière pour étudier les plantes du passé. La science, au travers de disciplines comme par exemple l'archéologie, la géologie, la géographie ou encore la génétique, permet dans une moindre mesure de franchir les barrières du temps. L'archéologie et la génétique nous ont permis de commencer à explorer et à décrire l'histoire évolutive des espèces cultivées (Meyer & Purugganan, 2013; Larson *et al.*, 2014). Récemment, l'écologie fonctionnelle a amené sa pierre à l'édifice en étudiant les changements phénotypiques qui ont opéré au cours de la domestication et de la sélection moderne, à la base de la performance des cultures (Milla *et al.*, 2015; Gómez-Fernández, 2023; Milla, 2023). Les pressions de sélection associées à la domestication et à l'amélioration variétale sont multiples et ont façonné la diversité génétique (Reif *et al.*, 2005; Glémin & Bataillon, 2009) et phénotypique (Milla & Matesanz, 2017) des espèces domestiquées mais aussi la diversité culturelle (pratiques, savoirs et usages, préférences alimentaires) associée à ces dernières (ex., diversité de la nomenclature traditionnelle d'une espèce cultivée, Article S1; Lemoine *et al.*, 2023). Reconstruire l'histoire des changements phénotypiques qui caractérisent les plantes cultivées est fondamental pour comprendre comment les interactions entre les plantes cultivées et leur milieu ont changé, et changent encore. Bien que la compétition intraspécifique dans les cultures occupe les agronomes depuis le milieu du XX^e siècle (Donald, 1968) et plus récemment les biologistes de l'évolution (Anten & Vermeulen, 2016), l'évolution des interactions entre plantes chez les espèces cultivées est encore mal connue (Fréville *et al.*, 2022). Les interactions intraspécifiques sont centrales pour l'établissement du rendement chez les espèces cultivées, mais aussi pour un ensemble d'autres fonctions nécessaires pour assurer une agriculture durable et résiliente (Litrico & Violle, 2015).

Basée sur l'exploration de données déjà acquises et de nouvelles expériences, cette thèse analyse (i) l'effet de la domestication et de la sélection moderne sur le phénotype du blé dur et les compromis qui le structurent, et (ii) comment les changements phénotypiques ont influencé la compétition intraspécifique pour les ressources. Nos résultats mettent en évidence que la variation phénotypique d'une espèce cultivée est contrainte par des compromis écophysiologiques classiquement observés à l'échelle interspécifique et par des lois allométriques. Ces contraintes et ces compromis persistent chez le blé dur malgré les pressions de sélection associées à la domestication et à l'amélioration variétale. Nous montrons par ailleurs des changements dans les stratégies écologiques entre les compartiments génétiques du blé dur. Nous observons une

meilleure aptitude à la compétition inter-génotypique des compartiments domestiqués par rapport au compartiment sauvage, malgré une plus forte plasticité des traits chez ce dernier. A l'inverse, nous montrons une invariance dans la réponse de la biomasse végétative et reproductive à l'augmentation de la densité entre les différents compartiments de la série de domestication du blé. Dans la suite, nous discutons du maintien des compromis et des contraintes allométriques au sein d'une espèce cultivée majeure en nous focalisant sur les questions suivantes : Comment ont été modulées les stratégies écologiques et l'aptitude à la compétition chez le blé dur ? Quels sont les mécanismes qui peuvent expliquer nos résultats : la sélection des traits d'intérêt agronomiques, le milieu des cultures, les contraintes entre les traits ?

I. Espace phénotypique et contraintes allométriques chez le blé dur, une plante comme les autres

Maintien des compromis fonctionnels chez une espèce cultivée

Le syndrome de domestication des plantes cultivées se caractérise principalement par des changements phénotypiques sur des traits en lien avec la structure reproductrice des plantes comme la taille de leurs graines, leur capacité de dispersion, leur dormance ou leur système de reproduction (Harlan *et al.*, 1976; Meyer *et al.*, 2012; Tanno & Willcox, 2012; Meyer & Purugganan, 2013). L'application récente de l'approche fonctionnelle pour étudier les changements phénotypiques des espèces cultivées a permis d'enrichir ce syndrome avec d'autres traits et notamment des traits associés à l'acquisition et à l'utilisation des ressources par les plantes (Milla *et al.*, 2015; Milla, 2023). L'écologie fonctionnelle permet d'étudier les liens entre les traits au sein du phénotype et de dépeindre les grands compromis écophysiologicals qui structurent la variation du vivant (Garnier *et al.*, 2016). Explorer le phénotype par une approche multivariée permet alors de capturer les interdépendances entre les traits qui peuvent contraindre son évolution. Ainsi, positionner les espèces ou les génotypes dans un espace phénotypique peut permettre de mieux appréhender les liens au sein du phénotype, les stratégies écologiques des espèces et de comprendre les mécanismes qui sous-tendent leur performance dans un environnement donné (Arnold, 1983; Laughlin & Messier, 2015). Mais qu'en est-il des espèces cultivées ? La domestication et l'amélioration variétale, ont-elles eu un effet sur la structuration de la variation phénotypique de ces espèces ?

De nombreuses études se sont attachées à caractériser le syndrome de domestication chez les plantes cultivées et à identifier ce qui les différenciait de leurs ancêtres sauvages (Harlan *et al.*, 1973; Fuller, 2007; Purugganan & Fuller, 2009; Meyer *et al.*, 2012; Fuller *et al.*, 2014). Cependant, peu d'études se sont intéressées aux changements dans les corrélations entre traits et dans la structure de l'espace phénotypique au cours de la domestication des plantes cultivées (Gagliardi *et al.*, 2015; Isaac *et al.*, 2017; Martin *et al.*, 2017; Roucou *et al.*, 2018; Xiong & Flexas, 2018; Cantarel *et al.*, 2020). La littérature documente principalement l'effet de la sélection humaine sur le compromis d'économie des ressources foliaires chez quelques espèces modèles comme le café, le riz, le soja ou le blé (Gagliardi *et al.*, 2015; Martin *et al.*, 2017; Xiong & Flexas, 2018; Hayes *et al.*, 2019). Dans le premier chapitre, en considérant à la fois des traits aériens et souterrains, nous explorons comment la variation phénotypique chez le blé dur se structure. Dans cette étude, nous mettons en évidence un espace fonctionnel structuré suivant les mêmes compromis que ceux observés à l'échelle interspécifique (Westoby *et al.*, 2002; Wright *et al.*, 2004; Reich, 2014; Díaz *et al.*, 2016; Weigelt *et al.*, 2021). Nous observons un premier axe communément décrit comme un gradient de stratégies d'exploration des sols, opposant des génotypes dont la stratégie est d'explorer le sol et d'acquérir les ressources grâce à des racines fines peu coûteuses à mettre en place, à des génotypes aux racines épaisses coûteuses en carbone mais supposées capables d'héberger des partenaires mycorhiziens en charge de l'acquisition d'une partie des ressources nécessaires à la plante (Eissenstat *et al.*, 2015; Kramer-Walter *et al.*, 2016; Bergmann & Weigelt, 2020; Weigelt *et al.*, 2021). Le deuxième axe de variation observé, illustre le compromis, à la fois racinaire et aérien entre le retour « rapide » ou « lent » sur l'investissement en carbone et en nutriments (Reich, 2014; Weigelt *et al.*, 2021). Cet axe oppose des génotypes dits « rapides » caractérisés par une forte teneur en azote foliaire (forte LNC) à des génotypes dits « lents » caractérisés par un tissu racinaire dense (forte RTD) et à forte masse foliaire par unité de surface (forte LMA, faible SLA) (Fig. 1, a). Ainsi, cet axe oppose des génotypes avec des feuilles et des racines bon marché, leur permettant un retour sur investissement rapide et de l'autre des génotypes avec des organes avec un coût de construction initial élevé et un long retour sur investissement. Les axes de variations observés dans le premier chapitre structurent également la variation phénotypique observée au sein de la série de domestication du blé dur (Fig. 1, b, données non publiées).

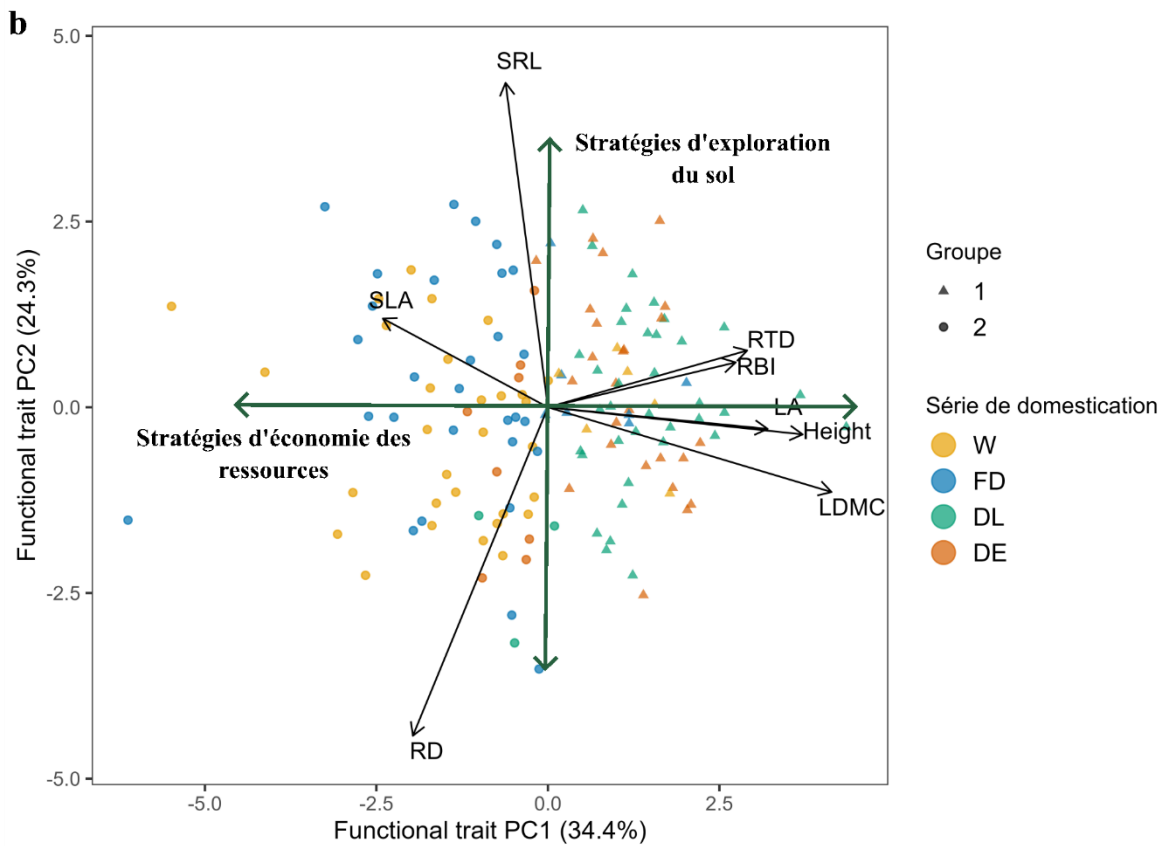
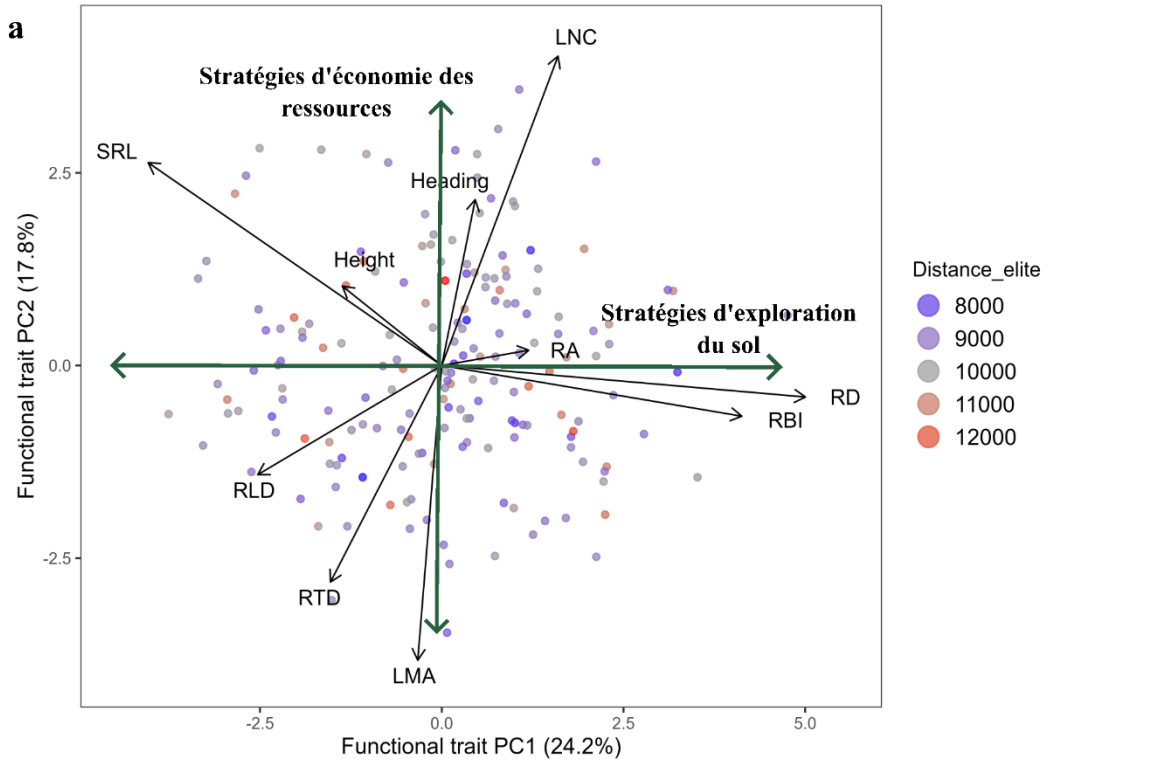


Figure 1. a) Projection des 179 lignées de blé dur EPO, et b) des mesures obtenues sur les 40 génotypes issus de la série de domestication du blé sur le plan défini par les deux premières composantes d'une analyse en composantes principales basée sur les caractères fonctionnels aériens et souterrains. Sur la figure (a), la couleur des points correspond à la distance génétique entre chaque génotype EPO et le compartiment élite du blé dur. Plus la couleur est violette, plus le génotype partage de similitudes alléliques avec le compartiment élite. Sur la figure (b), les génotypes ont été répartis en deux groupes dans l'ACP suivant une méthode de clustering (kmeans). Heading (degrés jours) : Date d'épiaison ; Height (cm) : hauteur maximale de la plante, LMA ($\text{kg}\cdot\text{m}^{-2}$) : surface de masse foliaire ; SLA ($\text{m}^2\cdot\text{kg}^{-1}$) ; LA (cm^2), surface foliaire ; LNC (%) : Teneur en azote des feuilles ; RA ($^\circ$) : Angle racinaire ; RBI (nombre de bouts par unité de longueur) : intensité de ramification des racines ; RD (mm) : Diamètre de la racine ; RLD ($\text{cm}\cdot\text{cm}^{-3}$) : densité de longueur des racines ; RTD ($\text{g}\cdot\text{cm}^{-3}$) : Densité du tissu racinaire et SRL ($\text{m}\cdot\text{g}^{-1}$) : Longueur spécifique de la racine. Rouge (W), ancêtres sauvages ; Jaune (FD), premières formes domestiquées ; Bleu (DL), variétés locales pré-Révolution Verte ; Vert (DE), variétés élites post-Révolution Verte.

Sur la base de nos résultats, nous montrons donc que la variation phénotypique observée chez une espèce cultivée n'est pas structurée différemment de celle observée chez les espèces sauvages, et ce, malgré les pressions de sélection associées à la domestication et à la sélection moderne. En effet, nous retrouvons les grands compromis fonctionnels mis en évidence à l'échelle interspécifique. Pourtant, une réduction de la force des liens entre les traits a été observée chez plusieurs espèces cultivées d'herbacées notamment après la sélection moderne (Milla *et al.*, 2014), par exemple une réduction des covariations entre le spectre d'économie des ressources foliaires et certains traits racinaires (Roucou *et al.*, 2018). Dans certaines études, la sélection artificielle a également modifié les syndromes de traits (Xiong & Flexas, 2018; Cantarel *et al.*, 2020). Par exemple, dans l'étude de Cantarel *et al.*, (2020), la relation forte entre la surface spécifique foliaire et la teneur en azote foliaire chez le blé n'a pas été détectée. L'absence de certains compromis ou les changements de certaines corrélations de traits chez d'autres espèces cultivées pourraient s'expliquer par une plus faible variation phénotypique chez certaines espèces cultivées ou des pressions de sélection différentes qui ont opéré sur ces espèces (Cantarel *et al.*, 2020; Milla, 2023). Par exemple, la variation des conditions environnementales des milieux cultivés depuis des millénaires a pu entraîner de nouvelles associations dans les traits ou au contraire éliminer certaines covariations entre traits impliqués dans les stratégies d'économie des ressources (Milla *et al.*, 2014, 2015).

D'après nos résultats, les compromis fonctionnels contraignent la variation phénotypique intraspécifique du blé dur, dans la mesure où les individus se positionnent le long de ces compromis écophysologiques. L'adaptation au milieu cultivé et la sélection humaine chez le blé dur ont entraîné des changements dans les valeurs de traits sans pour autant moduler les interdépendances entre les traits possiblement en raison de l'architecture génétique sous-jacente aux traits ou des contraintes écophysologiques et biomécaniques fortes entre les traits (Denison, 2015; Colombo *et al.*, 2022; Garland *et al.*, 2022).

Contraintes allométriques

Bien que variable, le phénotype des plantes est caractérisé par des relations trait-taille constantes entre plusieurs taxons (Enquist *et al.*, 1999; Brown *et al.*, 2004). L'invariance des paramètres allométriques découlerait de contraintes exercées par des lois biophysiques et biomécaniques sur les relations trait-taille (West *et al.*, 1997, 1999; West & Brown, 2005). Récemment, la variabilité, entre les espèces ou au sein des espèces, des paramètres allométriques a questionné le rôle de la sélection naturelle dans la modulation des contraintes allométriques (Poorter *et al.*, 2015; Vasseur *et al.*, 2018; Glazier, 2022). Mais qu'en est-il de la sélection artificielle ? Il existe relativement peu d'études qui explorent l'effet de la sélection artificielle sur les contraintes allométriques (ex. Egset *et al.*, 2012; Pélabon *et al.*, 2014; Voje *et al.*, 2014; Roucou, 2018).

Dans nos travaux, au travers d'une approche expérimentale, nous montrons que la biomasse reproductive des génotypes issus de la série de domestication du blé dur est fortement contrainte par la biomasse végétative atteinte par la plante. Cette relation découle des contraintes allométriques qui s'exercent sur l'allocation à la reproduction chez les plantes (Weiner, 2004; Qin *et al.*, 2013). Dans le premier chapitre, nous montrons une empreinte de la sélection artificielle sur l'espace agronomique du blé dur, confirmant un effet de la sélection artificielle sur les traits d'intérêt agronomique (Harlan *et al.*, 1973; Hay, 1995; Royo *et al.*, 2007, 2021; Peng *et al.*, 2011). Les génotypes partageant davantage de similitudes génétiques avec les variétés modernes étaient plus productifs et allouaient une plus forte proportion de ressources à la biomasse reproductive. En effet, chez les céréales utilisées pour leur grain, la sélection artificielle a majoritairement ciblé des traits ou des combinaisons de traits dans le but d'améliorer le rendement en grain et limiter la verse (Donald & Hamblin, 1976; Hay, 1995; Sadras *et al.*, 2011; Hill & Li, 2016). Nous montrons pourtant dans le troisième chapitre que l'allocation à la reproduction n'a pas varié au cours de la

domestication et de la sélection moderne du blé. Ces résultats suggèrent que les contraintes allométriques qui s'exercent sur l'allocation à la reproduction ne sont pas facilement modulables, même par la sélection artificielle. La domestication et la sélection moderne ont ainsi possiblement modifié davantage les valeurs moyennes du phénotype et moins les contraintes allométriques entre les traits. Egset *et al.*, (2012) ont tenté de sélectionner artificiellement et indépendamment la pente et l'ordonnée à l'origine de la relation allométrique entre la taille de la nageoire caudale et la taille du corps chez des guppys mâles. Ils ont montré que l'ordonnée à l'origine de la relation avait bien varié avec la sélection contrairement à la pente allométrique qui elle n'avait pas changé, suggérant une faible évolutivité de la pente allométrique. Ils proposent notamment que la sélection sur la pente est moins efficace que la sélection sur l'ordonnée à l'origine car elle ne correspond pas à une sélection directionnelle sur les traits sous-jacents (c'est-à-dire la taille du corps et la taille de la nageoire caudale). Nous manquons encore de connaissances sur l'effet de la sélection artificielle sur les relations allométriques et les mécanismes génétiques ou biophysiques qui sous-tendent ces changements. Dans le chapitre trois, nous trouvons par ailleurs que la relation entre la densité d'individus et la biomasse végétative ou reproductive ne varie pas entre les compartiments issus de la série de domestication du blé. Cette invariance, pourrait en particulier résulter de contraintes allométriques sur la croissance, similaires entre les génotypes en réponse à une forte densité de plantes (Deng *et al.*, 2012b). En effet, des relations d'échelle entre le taux métabolique et la densité de population ainsi que la biomasse végétale individuelle ont été mis en évidence (Deng *et al.*, 2008). Le blé quel que soit son compartiment génétique est probablement marqué par les mêmes contraintes sur son métabolisme et par conséquent sur sa biomasse végétative en réponse à la densité. Les contraintes allométriques semblent donc avoir une implication majeure pour le rendement final constant des cultures (Weiner & Freckleton, 2010; Deng *et al.*, 2012a). L'allométrie constitue également une limite importante pour l'optimisation de la densité dans les parcelles cultivées (Deng *et al.*, 2012a; Qin *et al.*, 2013). L'approche allométrique a aussi un fort potentiel pour caractériser les changements dans les stratégies écologiques des plantes (Gómez-Fernández, 2023). En effet, l'adaptation des espèces au milieu cultivé dans les agrosystèmes issus de la Révolution Verte, riches en ressources et perturbés, a aussi pu conduire à des changements dans les relations trait-taille.

Pour conclure cette première partie, nos résultats révèlent que le blé dur est marqué par les mêmes compromis écophysiologiques observés à l'échelle interspécifique et par des contraintes allométriques qui ne varient pas au cours de sa domestication et de la sélection moderne. Le blé dur, d'après nos résultats, semble donc être une plante comme les autres du point de vue des contraintes et des compromis qui structurent son phénotype. Il y a ainsi un réel enjeu pour la sélection de considérer les interdépendances entre les traits pour potentiellement les outrepasser (Denison *et al.*, 2003; Denison, 2015; Rolhauser *et al.*, 2022). Enfin, le blé a subi des changements phénotypiques importants tout au long de son histoire évolutive qui l'ont potentiellement déplacé le long de ces compromis.

II. Du phénotype à la compétition entre plantes chez le blé dur : effet de la domestication et de la sélection moderne

Changements dans les stratégies écologiques chez le blé dur

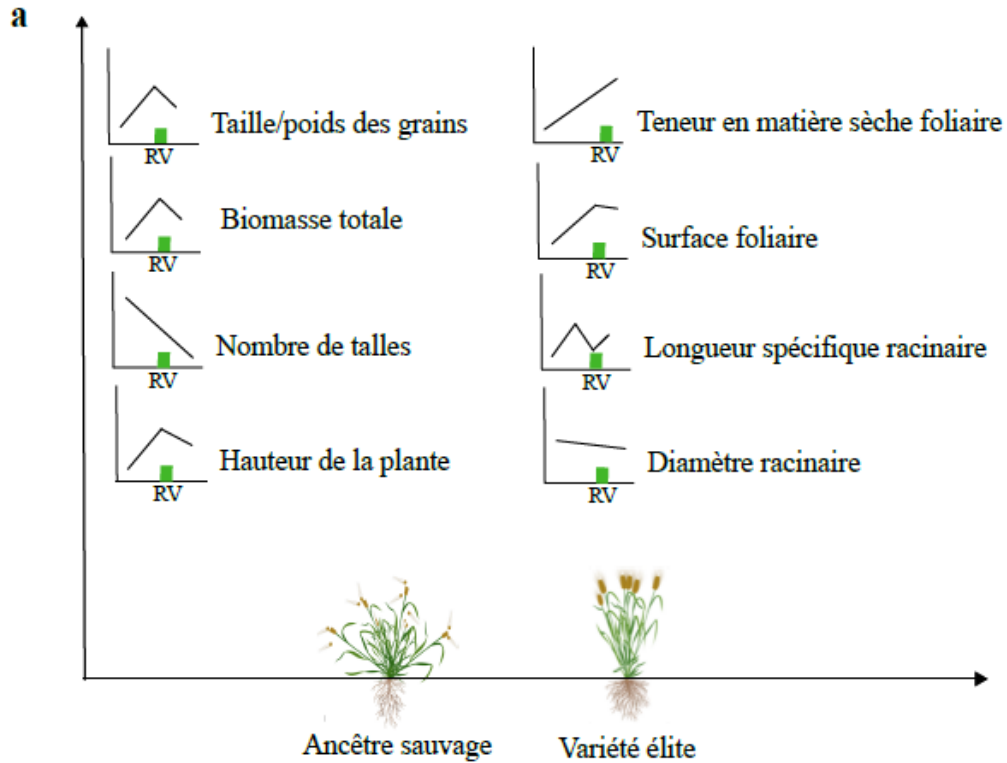
Pour comprendre les changements phénotypiques qui ont opéré au cours de l'histoire des cultures, il est important de rappeler ce qui les distinguait du reste du pool d'espèces sauvages aussi présentes il y a 10 000 ans. Quelques études ont montré que les ancêtres sauvages des cultures en comparaison d'autres espèces herbacées sauvages présentes dans les aires géographiques d'origine des cultures, avaient une plus grande stature (Cunniff *et al.*, 2014), une plus grande taille de graine et de biomasse en grain (Preece *et al.*, 2015) ou encore un plus fort investissement dans la reproduction en conditions de peuplement dense (Preece *et al.*, 2018). Les travaux récents de thèse de Gómez-Fernández (2023) ont également enrichi les connaissances sur les ancêtres sauvages des cultures annuelles. L'auteure a montré que ces derniers avaient une forte teneur en azote foliaire et une forte conductance stomatique, révélant des activités photosynthétiques et métaboliques plus élevées chez les ancêtres sauvages par rapport aux autres espèces sauvages herbacées annuelles. L'ensemble de ces résultats conforte l'idée d'une position des ancêtres sauvages des cultures à l'extrémité acquisitive du spectre d'économie des ressources foliaire et racinaire (Wright *et al.*, 2004; Bergmann & Weigelt, 2020). Les ancêtres sauvages des cultures auraient donc une tendance à être plutôt des espèces rudérales et/ou compétitrices (Gómez-Fernández, 2023). Les traits favorisant l'adaptation des ancêtres des cultures aux lieux de vie humains, milieux riches en

nutriments et en eau, et perturbés, auraient conduit à favoriser la domestication de ces espèces plus performantes dans ces environnements (Engelbrecht, 1916 dans Zeven, 1973). Toutefois, on dispose encore de peu d'informations sur l'évolution des stratégies écologiques des espèces cultivées. En particulier, il n'existe, à notre connaissance, aucune étude empirique qui caractérise l'aptitude à la compétition des espèces cultivées au cours de leur histoire évolutive. Dans cette thèse, l'étude comparative de génotypes de blé dur allant du compartiment sauvage aux variétés élites actuelles, nous a permis d'explorer l'effet de la domestication et de la sélection moderne sur son phénotype, ses stratégies écologiques et son aptitude à la compétition (Fig. 1, b & Fig. 2).

D'après l'espace phénotypique construit à partir de la série de domestication du blé, nous observons des différences dans les stratégies écologiques d'économie des ressources qui semblent se structurer suivant le premier axe de variation (Fig. 1, b). Nous trouvons un premier groupe (à droite ; Fig. 1, b), composé des variétés locales et des blés modernes, qui investissent davantage dans leur structure et dans leur tissu aérien et racinaire (forte LDMC, forte RTD, forte LA, forte hauteur). Un second groupe (à gauche, Fig. 1, b), majoritairement composé de génotypes sauvages et des premières formes domestiquées, se caractérise par des stratégies racinaires et foliaires plus acquisitives (forte SLA, faible RTD, faible LDMC). Les différences de valeurs de traits foliaires entre ces deux groupes pourraient découler de l'augmentation de la biomasse des plantes avec la domestication, qui du fait des relations allométriques au sein de la plante, aurait conduit à un élargissement des feuilles et à un investissement dans la structure foliaire (Milla & Matesanz, 2017) (Fig. 2a). Ce résultat contraste toutefois avec les attendus en termes de stratégies d'économie des ressources foliaires des espèces cultivées. En effet, d'après la littérature, il y aurait une tendance des espèces domestiquées à exprimer des traits associés à une acquisition et une utilisation rapide des ressources à savoir un taux de photosynthèse plus important, des teneurs en azote foliaire plus forte ou encore des surfaces spécifiques foliaires plus grandes par rapport à leurs ancêtres sauvages (Milla *et al.*, 2014; Roucou *et al.*, 2018; Gómez-Fernández, 2023). L'adaptation au milieu de cultures, hautement fertilisé et compétitif, expliquerait notamment les changements dans les stratégies foliaires et racinaires des espèces cultivées vers une acquisition et une utilisation efficace et rapide des ressources. Nous n'avons par ailleurs pas détecté de changements directionnels dans les stratégies d'exploration du sol (Fig. 1, a & Fig. 1, b & Fig. 2). Nous avons montré des changements morphologiques des racines chez les premières formes domestiquées du blé. Ce

compartiment investissait dans un système racinaire plus extensif et peu coûteux en carbone (forte longueur spécifique racinaire, faible densité de tissu racinaire), qui pourrait lui permettre une acquisition efficace des ressources du sol. Ces valeurs de trait ont été montrées comme associées à une aptitude à la compétition plus forte chez les herbacées sauvages (Mommer *et al.*, 2011). L'effet de la domestication sur les traits racinaires reste encore peu étudié, malgré le rôle central de l'architecture racinaire dans l'exploration du sol et la capture des nutriments (Lynch, 1995, 2013). Récemment, il a été montré que la domestication aurait favorisé une augmentation des racines fines permettant une exploration intensive du sol par les variétés modernes (Roucou *et al.*, 2018). Au contraire, Isaac *et al.*, (2021) ont montré que les traits racinaires des cultures (riz, maïs) étaient plus conservateurs (large diamètre racinaire, faible longueur spécifique racinaire) avec la domestication. Les traits racinaires des plantes cultivées peuvent donc varier de manière idiosyncratique avec la domestication (Martín-Robles *et al.*, 2019). De nombreux autres traits racinaires comme la densité de poils absorbants, le nombre de racines latérales ou encore l'angle des racines axiales paraissent également pertinents pour étudier les stratégies d'acquisition des nutriments par les plantes cultivées (York *et al.*, 2013). Il a notamment été montré que les types non-mutés du modèle *Arabidopsis thaliana*, produisant une forte densité de poils absorbants, avaient une meilleure aptitude à la compétition que les mutants utilisés sans poils, dans des milieux à faible teneur en phosphore (Bates & Lynch, 2001). Il y a donc probablement d'autres traits racinaires qu'ils seraient intéressants d'intégrer pour mieux explorer les changements dans les stratégies d'exploration et d'acquisition des ressources du sol au cours de la domestication.

Enfin, l'absence de changements directionnels des traits racinaires peut aussi s'expliquer par les conditions d'expérience en pot. Le volume du pot contraint fortement la croissance et la taille du système racinaire et donc probablement les stratégies racinaires que l'on peut observer (Poorter *et al.*, 2012; Freschet *et al.*, 2021). Le compartiment souterrain des espèces cultivées depuis leur état sauvage a dû s'adapter à différents environnements de culture et peut constituer un véritable couteau suisse pour la résilience des cultures face aux changements globaux. Cependant, le compartiment racinaire est très plastique, donc dépendant du contexte environnemental dans lequel sont effectuées les mesures (Hodge, 2004). Par ailleurs, le système racinaire est aussi complexe à caractériser : quels traits choisir, quelles racines choisir, quand et dans quelles conditions les mesurer (pot, champ), sont des questions qui partagent la communauté scientifique et qui ne sont pas encore résolues (Fort, 2023).



b Variation du poids d'un grain (g)

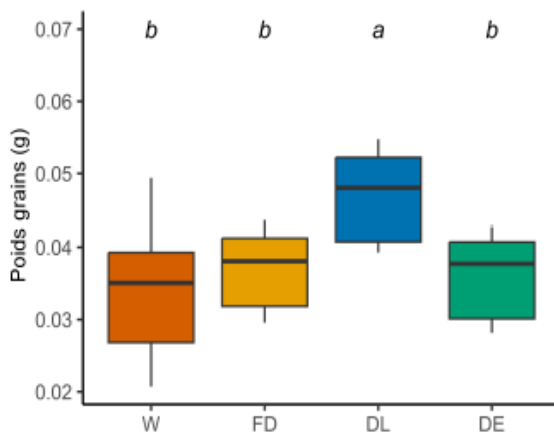


Figure 2. a) Présentation synthétique de la variation des traits, observés chez le blé dur en conditions de plante isolée au cours de sa domestication et de la sélection moderne. RV (rectangle vert) indique la période de la Révolution Verte. Les résultats se basent sur les mesures de traits effectuées dans les chapitres 2 & 3. b) Variation du poids moyen d'un grain entre les différents compartiments génétiques du blé. Cinq grains ont été pesés par génotype. Les lettres montrent les différences significatives entre les compartiments génétiques. Rouge (W), ancêtres sauvages ; Jaune (FD), premières formes domestiquées ; Bleu (DL), variétés locales pré-Révolution Verte ; Vert (DE), variétés élites post-Révolution Verte.

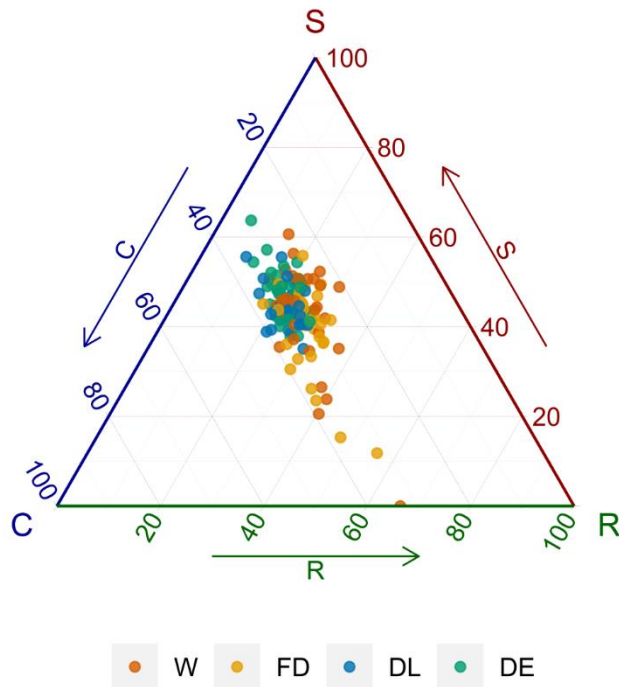


Figure 3. Superposition des scores CSR sur un triangle de Grime obtenu dans le chapitre 2 à partir des traits foliaires. Le premier axe sépare les génotypes compétiteurs (C) des génotypes tolérants aux stress (S). Cet axe peut être interprété comme un axe de gestion des ressources opposant d'un côté les compétiteurs qui ont un fort besoin en ressources et de l'autre des génotypes (S) capables de mieux tolérer le stress (croissance lente). Le second axe est un axe de tolérance à l'intensité de perturbation. Il oppose des génotypes qui ne tolèrent pas les perturbations, aux génotypes qui la tolèrent. Cet axe est souvent interprété comme un axe de compromis entre taille et nombre de graines (Westoby *et al.*, 2002), illustrant le compromis entre colonisation et compétition chez les plantes. Les plantes rudérales comme les espèces cultivées ont généralement un cycle court et produisent beaucoup de petites graines. Rouge (W), ancêtres sauvages ; Jaune (FD), premières formes domestiquées ; Bleu (DL), variétés locales pré-Révolution Verte ; Vert (DE), variétés élités post-Révolution Verte.

Pour résumer les changements des stratégies écologiques, nous avons placé les scores CSR (Grime, 1977) des différents génotypes issus de la série de domestication dans un triangle de Grime (Fig. 3). Nous avons détecté que les ancêtres sauvages et les premières formes domestiquées chez le blé avaient un score R plus fort que les variétés locales et les variétés élités ($P < 0.05$). Nous n'avons pas observé de différences dans les scores C du triangle de Grime entre les compartiments. Nous avons détecté des différences dans les scores S entre les premières formes domestiquées et les blés

élites ($P < 0.01$). Sur la base de nos résultats, les génotypes sauvages et les premières formes domestiquées chez le blé paraissent plutôt rudéraux et compétitifs (forte SLA), probablement en raison de leur adaptation à des milieux très perturbés et fertiles comme les lieux de vie humains, puis aux premières pratiques agricoles. Avec l'expansion agricole, le blé dur a ensuite dû s'adapter à des conditions plus compétitives et stressantes en ressources, potentiellement dû à l'augmentation de la densité dans les parcelles cultivées, les faisant basculer vers une stratégie davantage stress tolérante (forte LDMC) et compétitive (forte hauteur et surface foliaire).

Évolution de l'aptitude à la compétition chez le blé dur

Dans ce travail, nous avons montré une augmentation de la biomasse aérienne (Fig. 2, a). La domestication a conduit également à un changement dans l'occupation de l'espace chez le blé avec une occupation en hauteur du compartiment aérien plutôt qu'en largeur (diminution du nombre de talles) (Fig. 2, a). L'augmentation de la biomasse aérienne, de la surface foliaire et de la hauteur chez les espèces cultivées a été observée chez différentes espèces (Milla & Matesanz, 2017; Gómez-Fernández, 2023). L'augmentation de la taille des espèces cultivées pourrait notamment s'expliquer par l'augmentation de la taille des graines au cours de la domestication (Fig. 2, b). De grosses graines donnent lieu à des plantules plus larges (Westoby *et al.*, 1992), amenant à un agrandissement général des organes du fait des contraintes allométriques au cours de la croissance (Milla & Matesanz, 2017). La taille des graines et de la plante entière sont également des caractéristiques qui améliorent l'aptitude à la compétition pour la ressource lors de l'établissement de la plantule et de sa croissance (Gaudet & Keddy, 1988; Westoby *et al.*, 1992; Kunstler *et al.*, 2016). Nous avons d'ailleurs montré dans le chapitre 2 une meilleure aptitude à la compétition des premières formes domestiquées et des variétés locales par rapport au compartiment sauvage. Les variétés locales en particulier avaient de grosses graines (Fig. 2, b), étaient très grandes et développaient de larges feuilles avec une forte teneur en matière sèche. En compétition, les individus ont tendance à surinvestir dans des structures de support en allongeant leur tige ou leurs surfaces foliaires pour capturer les ressources au détriment de leur voisin (Sorrensen-Cothorn *et al.*, 1993; Aphalo *et al.*, 1999). Les conditions de culture semblent avoir favorisé l'expression de ces stratégies, amenant à une augmentation de la compétition intraspécifique dans les systèmes

cultivés au cours de la domestication, décrivant une situation de Tragédie des Communs (Hardin, 1968; Weiner, 2003; Anten & Vermeulen, 2016).

Depuis le milieu du XX^{ème} siècle, l'effet de la compétition intraspécifique dans les cultures sur le rendement a été considéré. Donald a amené l'idée qu'une plante individuelle pourrait exprimer son potentiel de productivité pleinement si ses voisins exerçaient un faible effet compétiteur (n'accaparaient pas les ressources); il a ainsi proposé pour les céréales de cibler en sélection un idéotype du « faible compétiteur » ou « idéotype communal » caractérisé notamment par une stature réduite, un faible nombre de talles et des feuilles érigées (Donald, 1968). Ainsi, la sélection moderne a favorisé des phénotypes de petite stature, peu compétiteurs, maximisant la productivité du peuplement et non plus la productivité individuelle (Weiner, 2003; Weiner *et al.*, 2010). Ces changements expliqueraient d'ailleurs que les variétés modernes toléreraient mieux des conditions de forte densité comparativement aux autres stades de domestication, leur permettant une meilleure productivité en peuplement monogénotypique (Postma *et al.*, 2021). Cependant, dans nos travaux, nous n'avons pas détecté de différence, entre les compartiments domestiqués (premières formes domestiquées, variétés locales, variétés élites) dans la réponse à la compétition inter-génotypique (chapitre 2). De plus, nous trouvons que le blé dur élite subit la même réduction en biomasse que les autres compartiments domestiqués en réponse à la densité (chapitre 3). Ce résultat suggère que les variétés post-Révolution Verte ont la même capacité à tolérer la réduction de la disponibilité en ressources due au voisinage que les autres compartiments domestiqués et ce, malgré la sélection artificielle sur plusieurs traits relatifs à l'aptitude à la compétition (hauteur, nombre de talles, surface foliaire). De plus, nous n'avons pas détecté de différences dans la réponse à la compétition intra-génotypique (chapitre 3) entre les ancêtres sauvages du blé dur et ses formes domestiquées, contrairement aux résultats de l'expérimentation de compétition inter-génotypique (chapitre 2).

Dans le chapitre 2, nous avons établi artificiellement un premier environnement où les compartiments domestiqués et le compartiment sauvage étaient en compétition avec une variété élite. Cet environnement artificiel très compétitif et dense constituait un environnement dans lequel les compartiments domestiqués ont évolué et qui a façonné leur phénotype en réponse notamment à la compétition. A l'inverse, dans notre expérimentation, les génotypes du compartiment sauvage du blé se sont retrouvés dans un environnement de compétition inexistant dans l'environnement naturel, au sein duquel ils ont probablement évolué en peuplement monospécifique du fait de leur dispersion naturelle de proche en proche (Harlan, 1967; Ladizinsky, 1975). Dans ce premier

environnement expérimental, nous avons observé que malgré une plus forte plasticité phénotypique, les génotypes sauvages subissaient fortement la compétition. Nous avons par exemple détecté qu'une même valeur de plasticité en hauteur des génotypes sauvages et des variétés locales, conduisaient à une meilleure performance en réponse à la compétition des variétés locales. Comme proposé dans DeWitt *et al.*, (1998), induire une réponse plastique nécessite d'acquérir des informations sur l'environnement. Parfois, les organismes fixés et spécialistes d'un type d'environnement, une fois placé dans un environnement alternatif, peuvent ne pas détecter le bon signal environnemental ou parfois trop tardivement (Getty, 1996). Ceci peut amener à un décalage ou « mismatch » entre le phénotype et l'environnement (mal-adaptation) qui limite sévèrement les bénéfices de la plasticité (DeWitt *et al.*, 1998). Les génotypes sauvages se trouvent potentiellement dans cette situation de « mismatch » environnemental. Ils ne sont probablement pas adaptés à cet environnement de compétition et ils n'ont pas le phénotype et la plasticité pour tolérer un tel environnement. À l'inverse, dans l'expérience de densité, ils se retrouvent dans des conditions environnementales qui se rapprochent probablement plus de celles de leur « milieu naturel ». De plus, les compartiments domestiqués et les ancêtres sauvages du blé n'ont pas le même phénotype et les différences phénotypiques avec leur concurrent peuvent conduire à de la compétition asymétrique, c'est-à-dire à un effet de dominance d'une plante sur l'autre (Weiner, 1990). La hauteur individuelle, par exemple, influence l'interception de la lumière, un processus clé en compétition, où les plantes plus hautes ont un avantage concurrentiel (Violle *et al.*, 2009; Carmona *et al.*, 2019). La compétition asymétrique entre les génotypes sauvages du blé et la variété élite pourrait expliquer la plus faible performance du compartiment sauvage en conditions de compétition inter-génotypique par rapport aux conditions intra-génotypiques (Fig. 4). D'après la fig. 4b, les génotypes sauvages du blé sont en moyenne plus performants avec eux-mêmes qu'avec un génotype élite, donc très différent phénotypiquement. En situation de compétition inter-génotypique, les génotypes du compartiment sauvage avaient en effet un désavantage car ils étaient plus tardifs et plus petits que le compétiteur, créant une asymétrie temporelle et spatiale dans la compétition pour la ressource (Freckleton & Watkinson, 2001). Ce point est également une limite du chapitre deux. En effet, nous avons analysé la réponse à la compétition de la série de domestication du blé dur avec un génotype voisin unique dans l'expérimentation, pour des questions de dimensionnalité de l'expérience. Dans des expériences futures, il serait intéressant de tester l'effet de l'identité fonctionnelle du voisin sur la réponse à la compétition du blé au cours de

sa domestication et de l'amélioration variétale. Cela pourrait permettre d'identifier des associations de variétés modernes ou anciennes dont les combinaisons de trait diminueraient le niveau de compétition pour la ressource dans le milieu.

Sur la base de nos résultats, les ancêtres sauvages du blé ont une plus faible aptitude à la compétition que les premières formes domestiquées et les variétés locales domestiquées. Les blés domestiqués sont adaptés à un milieu très dense et compétitif qui a sélectionné des stratégies à la fois spatiale (encombrement spatial) et temporelle (traits acquisitifs (SLA et SRL forte) chez les premières formes domestiquées) leur permettant d'acquérir et d'utiliser les ressources plus rapidement et plus efficacement que les blés sauvages. Il serait intéressant de mener une expérience complémentaire pour évaluer les changements dans « l'effet compétiteur » (c.-à-d. la capacité à réduire la performance de son voisin), le second aspect de l'aptitude à la compétition, car il est fort probable qu'au regard des traits aériens sélectionnés, les variétés post-Révolution Verte expriment un plus faible effet compétiteur que les autres compartiments domestiqués. La question de l'asymétrie dans la compétition pour la ressource demanderait d'être mieux approfondie car les implications de ce mécanisme dans la réponse à la densité des cultures et dans leur rendement sont importantes (Weiner & Freckleton, 2010; Barot *et al.*, 2017). En effet, l'asymétrie de la compétition entre individus agit sur la forme de la réponse à la densité et par conséquent sur le rendement final constant (Freckleton & Watkinson, 2001). Par ailleurs, si le trait de réponse est plastique, l'asymétrie dans la compétition amène aussi à un investissement de l'individu dans de la plasticité pour minimiser son désavantage (Xiao *et al.*, 2006) au détriment d'un investissement de la ressource dans d'autres fonctions comme la reproduction.

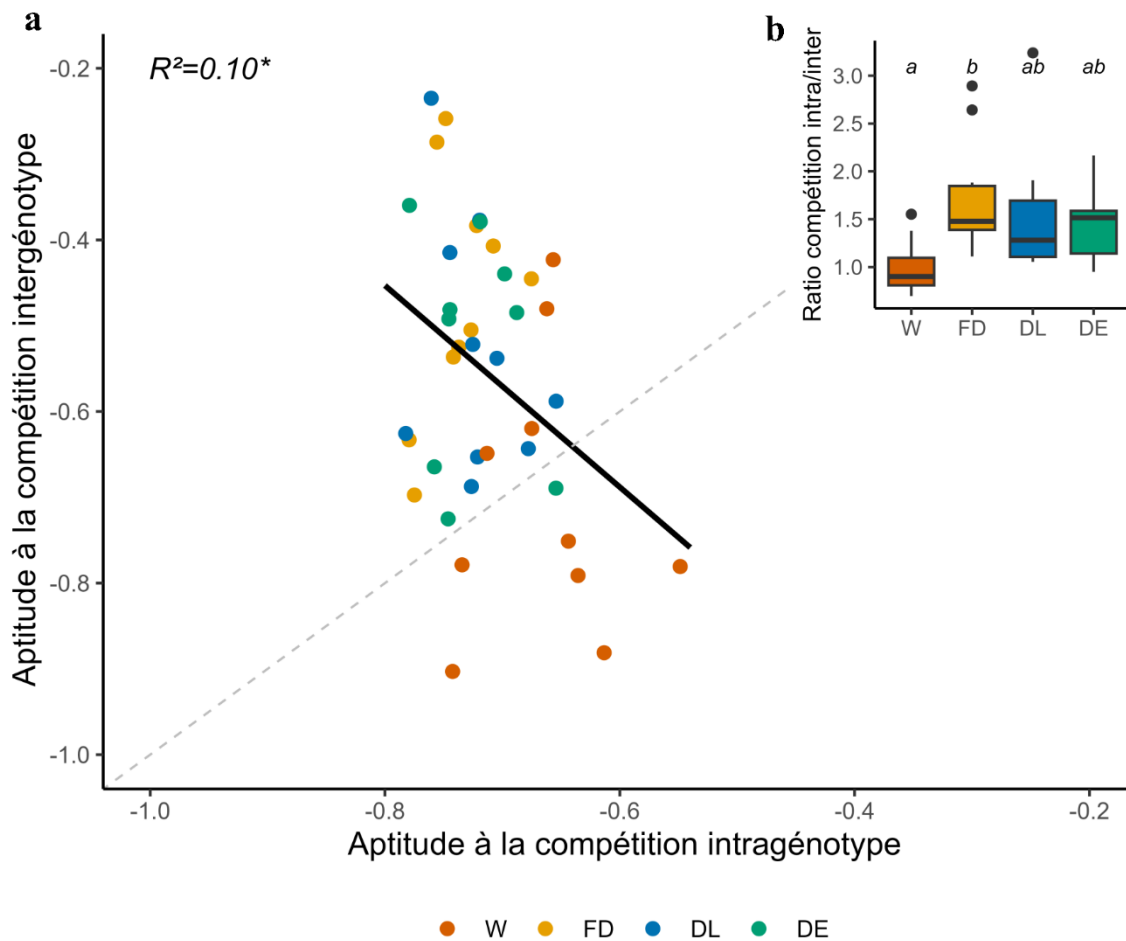


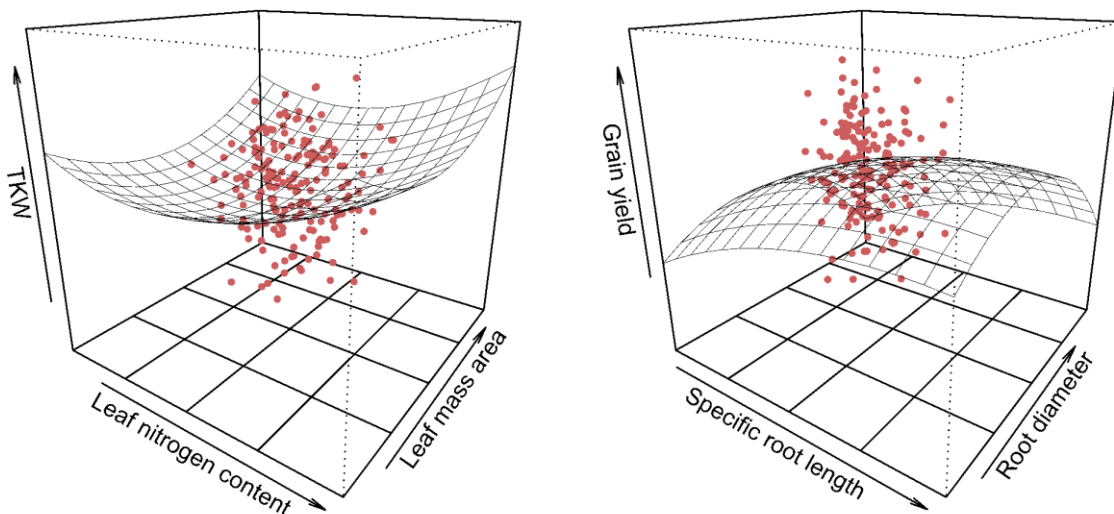
Figure 4. a) Relation entre l’aptitude à la compétition mesurée sur un individu en peuplement mono-génotypique ou sur un individu en conditions de compétition avec un génotype élite dans les mêmes conditions de densité de plantes (5 individus par pot). L’aptitude à la compétition a été estimée en faisant la différence entre la valeur de la biomasse végétative pour chaque génotype en compétition et en condition isolée divisée par la valeur de la biomasse totale en condition isolée. Une valeur négative indique donc que le génotype a perdu de la biomasse en réponse à la compétition. Des moyennes ont été faites par génotypes. b) Comparaison des moyennes et de la variation des ratios entre aptitude à la compétition intra-génotypique sur l’aptitude à la compétition inter-génotypique entre les différents compartiments de la série de domestication du blé. Rouge (W), ancêtres sauvages ; Jaune (FD), premières formes domestiquées ; Bleu (DL), variétés locales pré-Révolution Verte ; Vert (DE), variétés élites post-Révolution Verte. Le coefficient de régression ajusté (R^2) est présenté, ainsi que l’analyse de variance ($P = 0.03$).

PERSPECTIVES

I. Les traits fonctionnels pour prédire la performance agronomique ?

La sélection par « idéotype » a permis de ne plus uniquement sélectionner une variété sur sa productivité mais aussi de considérer des traits architecturaux (hauteur, surface foliaire) étroitement liés à sa photosynthèse, sa croissance et sa production en grains (Donald, 1968). La performance d'une plante reste cependant compliquée à prédire car elle est liée à une multitude de traits qui covarient les uns avec les autres (Violle *et al.*, 2007). Dans le premier chapitre, nous avons identifié des combinaisons de traits aériens et souterrains liées à la performance agronomique de différents génotypes de blé dur (productivité en grain, indice de récolte, poids de mille grains). Ces résultats ont permis de montrer que les traits impliqués dans la variation de la performance agronomique chez le blé étaient portés par différents axes de variation impliquant l'entière du phénotype des plantes (Encadré 1).

Encadré 1 - Traits fonctionnels et performance agronomique



- **Plusieurs combinaisons phénotypiques** peuvent amener à la **même performance agronomique** au niveau de la parcelle
- Plusieurs traits doivent être ciblés simultanément à l'échelle du **phénotype entier**

La multidimensionnalité des relations traits-performance implique des interactions entre plusieurs traits écophysiologicals et biomécaniques au sein de la plante et peut potentiellement conduire à plusieurs optimums dans la performance des plantes (Laughlin & Messier, 2015). Du fait de la non-linéarité de certaines relations, différentes combinaisons de traits chez le blé peuvent aussi conduire à une même performance agronomique au champ (Koehl, 1996; Wainwright *et al.*, 2005) (Encadré 1). Ces résultats peuvent être intéressants pour la sélection variétale car plusieurs phénotypes peuvent amener à une même performance. Toutefois, la performance individuelle est fortement contexte-dépendante (Rolhauser *et al.*, 2022). La plasticité phénotypique peut jouer un rôle important dans la variation de la performance des plantes (MacLaren *et al.*, 2023). Dans le deuxième chapitre, nous avons testé si les traits mesurés sur des plantes en conditions isolées peuvent prédire la performance en compétition de nos génotypes comme proposée par l'approche basée sur les traits (Violle *et al.*, 2007; Shipley *et al.*, 2016). Nous avons ainsi montré que les traits en conditions isolés ne prédisaient pas la performance en compétition des génotypes. En revanche, nous avons démontré que les traits mesurés en conditions de compétition expliquaient une part importante de la performance des génotypes en compétition (respectivement, 27% et 20% pour la surface foliaire et la hauteur), comme déjà démontré dans Violle *et al.*, (2009). La performance d'une plante semble fortement dépendante de l'environnement biotique.

Malgré tout, les traits fonctionnels n'expliquaient qu'une faible part de la variation (entre 15% et 25%) de la performance agronomique (productivité en grain, indice de récolte, poids de mille grains ; chapitre 1). Nous avons démontré dans le chapitre 3 que la biomasse végétative expliquait une part importante de la variation de la biomasse reproductive (~80%). Le rendement des cultures peut en effet être efficacement prédit à partir de la biomasse sèche, l'indice de surface foliaire (LAI) ou encore la capacité photosynthétique (Marcelis *et al.*, 1998; Serrano *et al.*, 2000). Depuis quelques années, l'intelligence artificielle et de nombreuses données comme des images satellites, des données de capteurs, météo ou même collectées au champ sont utilisées pour prédire la performance des cultures à large échelle (Li *et al.*, 2020; Marshall *et al.*, 2022). L'écologie fonctionnelle a un large potentiel pour comprendre pourquoi et comment le phénotype varie dans un milieu donné et analyser les stratégies des espèces cultivées afin d'alimenter les connaissances pour la diversification des cultures. En effet, les interactions plante-plante impactent la performance de la parcelle en fonction des types d'interactions qui s'établissent (compétition, facilitation, complémentarité) (Barot *et al.*, 2017).

II. Diversifier le matériel végétal pour limiter la compétition ?

Les interactions de compétition pour la ressource entre plantes sont des interactions majeures dans les milieux cultivés. L'adaptation du blé aux conditions des milieux cultivés a favorisé l'expression de phénotype compétiteur maximisant leur performance individuelle dans un milieu riche en ressources (Weiner, 2003). Pour réduire le niveau de compétition intraspécifique dans les cultures, certains traits architecturaux (stature, surface et angle foliaires) ont été sélectionnés depuis les années 60s (Donald, 1968). Pourtant, nous n'avons pas montré de différences dans la réponse à la compétition inter- et intra-génotypique (chapitres 2 & 3) entre les variétés locales et les variétés élites chez le blé dur. Ainsi, malgré les efforts de la sélection moderne, certains traits (traits racinaires, teneur en silicium, exsudats racinaires) et certaines réponses plastiques du phénotype maximisant l'aptitude à la compétition pour la ressource, non mesurées dans nos travaux, doivent persister dans les cultures. Par exemple, il est fortement probable qu'il y a une plasticité racinaire en réponse au voisinage (ex. croissance, distribution des racines ; Callaway *et al.*, 2003) chez les variétés élites au cours de leur croissance et leur développement qui leur confère une meilleure aptitude à la compétition, en particulier du fait que l'amélioration variétale a principalement ciblé les organes visibles des plantes cultivées (Anten & Vermeulen, 2016). Une caractérisation plus fine des racines (anatomique, morphologique et physiologique) serait donc intéressante pour affiner l'étude des changements dans l'aptitude à la compétition des espèces cultivées au niveau racinaire. Cette analyse plus fine permettrait de trouver de la diversité phénotypique dans d'autres compartiments génétiques (formes sauvages, variétés locales) qui serait intéressante pour limiter la compétition intraspécifique souterraine et pour concevoir un idéotype racinaire pour les cultures monogénétiques (York *et al.*, 2013). Plus largement, explorer la diversité phénotypique et les stratégies écologiques dans les différents compartiments génétiques des espèces cultivées peut permettre de cibler des traits caractéristiques de faible compétiteur pour la ressource au niveau de la plante entière dans le but d'améliorer le rendement de la parcelle.

Une autre solution, déjà abordée dans la littérature, pour améliorer les fonctions des agrosystèmes comme la productivité, est de réintroduire de la variation phénotypique sur des traits liés aux effets positifs de biodiversité (complémentarité de niche⁷ et effet de sélection) (Montazeaud *et al.*, 2020;

⁷ La complémentarité de niche repose sur la capacité des espèces ou variétés à utiliser différentes ressources locales dans l'espace et le temps (Macarthur et Levins 1967; Litrico et Violle 2015).

Fréville *et al.*, 2022). La diversification des systèmes cultivés par le mélange de plusieurs espèces ou variétés, a déjà montré des effets positifs sur la stabilité et la productivité des cultures (Prieto *et al.* 2015 ; Barot *et al.* 2017 ; Borg *et al.* 2018 ; Montazeaud *et al.* 2020) mais aussi sur leur résistance aux pathogènes (Finckh *et al.* 2000 ; Péliissier *et al.* 2021). Certaines études ont cependant montré que les interactions positives de complémentarité de niche ont été réduites au cours de la sélection des cultures (Chacón-Labela *et al.*, 2019; Fréville *et al.*, 2022). Ceci résulterait notamment de l'uniformité phénotypique due à la réduction de la diversité génétique des cultures et d'une réduction de la plasticité phénotypique chez les espèces cultivées. En effet, la variation phénotypique et la plasticité phénotypique impactent les interactions de complémentarité entre espèces ou génotypes (Prieto *et al.*, 2015, 2017). Chacón-Labela *et al.*, (2019) ont notamment montré que les mélanges de cultures annuelles avaient une meilleure productivité si les espèces qui les composaient, présentaient des valeurs contrastées de traits fonctionnels clés comme la surface foliaire. Ils ont par ailleurs montré que les effets de biodiversité étaient beaucoup plus forts dans des associations plurispécifiques composées des ancêtres sauvages que dans des mélanges équivalents composés de formes domestiquées. Il y a donc potentiellement un grand intérêt à diversifier les peuplements cultivés avec du matériel végétal issu d'autres compartiments génétiques des cultures pour améliorer les fonctions des agrosystèmes (Prescott-Allen & Prescott-Allen, 1986; Dempewolf *et al.*, 2017; Zhang *et al.*, 2017).

Les effets positifs de la diversité dans ces études sont souvent expliqués par un fort effet de sélection (Montazeaud *et al.*, 2018; Chacón-Labela *et al.*, 2019; Tatsumi & Loreau, 2023). L'effet de sélection, traduit l'idée que des systèmes à forte diversité ont une forte probabilité de contenir des espèces ou variétés plus productives dans des conditions locales données, entraînant un accroissement de la productivité du système si celles-ci deviennent dominantes (Loreau, 1998; Hector, 1999). L'effet de sélection repose finalement sur des différences d'aptitude à la compétition entre les génotypes qui peuvent amener à plus de productivité de certains génotypes quand ils sont en compétition avec d'autres génotypes qu'eux-mêmes. Par exemple, dans la figure 4b, nous avons montré que les génotypes sauvages du blé sont plus performants avec eux-mêmes qu'avec un voisin différent. Au regard de la figure 4, nous pouvons imaginer qu'il y aurait un plus fort effet de sélection au sein des pots avec les génotypes sauvages du fait des différences d'aptitude à la compétition entre les génotypes sauvages et le génotype élite (chapitre 2). Pour la productivité des cultures, la compétition pour la ressource est un mécanisme central. Les stratégies écologiques des

formes sauvages peuvent être pertinentes pour diminuer la compétition dans les parcelles. Il reste toutefois un manque de connaissances sur la réponse des formes sauvages aux conditions abiotiques et biotiques, en particulier à différents voisins.

III. Aller plus loin dans l'étude de l'aptitude à la compétition

Sur la base de nos résultats, plusieurs pistes de recherche pourraient être développées pour affiner notre compréhension de l'évolution de l'aptitude à la compétition chez le blé dur. Nous avons montré dans ces travaux que la réponse à la compétition a variés au cours de la domestication et de la sélection moderne. Cependant, nous n'avons testé que deux conditions de compétition (inter-génotypique avec une variété élite et intra-génotypique). Premièrement, il serait intéressant de mener d'autres expériences de réponse à la compétition impliquant une série de domestication mais plusieurs voisins différents, par exemple un voisin issu de chaque compartiment de l'histoire de domestication du blé. On pourrait s'attendre, par exemple, à ce que l'ensemble des compartiments subissent beaucoup moins la compétition face à un ancêtre sauvage. L'aptitude à la compétition pourrait d'ailleurs être caractérisée via la mesure d'autres traits racinaires, impliqués dans l'exploration (taux de croissance racinaire, nombre de racines axiales ; York *et al.*, 2013), l'acquisition (poils absorbants) et la mobilisation de certains nutriments comme le phosphore (Lynch, 2011), qui pourraient affiner la compréhension des mécanismes associés à la compétition entre les plantes. Deuxièmement, il serait intéressant de mener de nouvelles expériences pour évaluer les changements dans « l'effet compétiteur » au cours de la domestication et de la sélection moderne, car au regard des traits qui sous-tendent l'idéotype du « faible compétiteur », les variétés élites sont potentiellement de meilleures voisines car elles accapareront moins les ressources lumineuses que les variétés locales. Cette nouvelle expérience consisterait à non plus faire varier le génotype « phytomètre » ou « focal » qui lui serait fixe, mais à faire varier les génotypes voisins qui appartiendraient aux différents stades de la série de domestication du blé dur. Troisièmement, il serait intéressant de faire également varier les niveaux de nutriments comme l'azote et le phosphore, deux éléments essentiels à la productivité des cultures (Krouk & Kiba, 2020). La forte plasticité du compartiment sauvage pourrait par exemple induire une meilleure aptitude à la compétition de ces derniers dans des conditions de compétition avec peu de ressources (Bradshaw, 1965; Sultan, 2003). Tester différentes conditions environnementales permettrait aussi d'évaluer

comment la plasticité a été modulée chez les espèces cultivées. Dans la littérature, il est suggéré que la plasticité phénotypique a probablement été contre-sélectionnée au cours de la domestication et de la sélection (Grossman & Rice, 2012; Des Marais *et al.*, 2013) et c'est une question qui n'est toujours pas résolue. Je trouve central de poursuivre les études sur l'évolution de l'aptitude à la compétition chez les espèces cultivées car les autres compartiments génétiques du blé peuvent constituer un réservoir de phénotypes intéressants pour limiter la compétition dans les agrosystèmes. Il serait par exemple envisageable de cibler des traits des ancêtres sauvages caractéristiques d'un phénotype faiblement compétiteur pour limiter la compétition dans les peuplements mono-génotypiques.

Pour finir, quantifier l'aptitude à la compétition des ancêtres sauvages des cultures donnerait des pistes pour comprendre pourquoi ces espèces cultivées ont été choisies par les êtres humains à l'époque. Sur la base des études archéobotaniques, il serait intéressant, par une approche expérimentale de reconstruire les conditions environnementales des lieux de vie humains du Néolithique (fertile, perturbée, humide, « tas d'ordures ») et des potentielles communautés de plantes au sein desquelles se trouvaient les ancêtres des cultures pour tester leur aptitude à la compétition. Si ces espèces sont belles et bien plus compétitives (taille de graine plus grande, fort taux de croissance ; Gómez-Fernández, 2023) que les autres espèces herbacées présentes dans le milieu, il y a de fortes chances qu'elles aient fini par dominer ces milieux. Pour l'exemple du blé, on pourrait s'attendre au bout de quelques générations à avoir des patches de blé sauvage et quelques espèces adventices persistantes.

IV. Bibliographie

- Anten NPR, Vermeulen PJ. 2016.** Tragedies and Crops: Understanding Natural Selection To Improve Cropping Systems. *Trends in Ecology & Evolution* **31**: 429–439.
- Aphalo PJ, Ballare CL, Scopel AL. 1999.** Plant–plant signalling, the shade-avoidance response and competition. *Journal of Experimental Botany* **50**: 1629–1634,.
- Arnold SJ. 1983.** Morphology, Performance and Fitness. *American Zoologist* **23**: 347–361.
- Barot S, Allard V, Cantarel A, Enjalbert J, Gauffreteau A, Goldringer I, Lata J-C, Le Roux X, Niboyet A, Porcher E. 2017.** Designing mixtures of varieties for multifunctional agriculture with the help of ecology. A review. *Agronomy for Sustainable Development* **37**: 1–20.
- Bates TR, Lynch JP. 2001.** Root hairs confer a competitive advantage under low phosphorus availability. *Plant Soil* **236**: 243:250.
- Bergmann J, Weigelt A. 2020.** The fungal collaboration gradient dominates the root economics space in plants. *Science Advances* **6**: 37–56.
- Borg J, Kiær LP, Lecarpentier C, Goldringer I, Gauffreteau A, Saint-Jean S, Barot S, Enjalbert J. 2018.** Unfolding the potential of wheat cultivar mixtures: A meta-analysis perspective and identification of knowledge gaps. *Field Crops Research* **221**: 298–313.
- Bradshaw AD. 1965.** Evolutionary Significance of Phenotypic Plasticity in Plants. In: Caspari EW, Thoday JM, eds. *Advances in Genetics*. Academic Press, 115–155.
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004.** Toward a Metabolic Theory of Ecology. *Ecology* **85**: 1771–1789.
- Callaway RM, Pennings SC, Richards CL. 2003.** Phenotypic Plasticity and Interactions Among Plants. *Ecology* **84**: 1115–1128.
- Cantarel AAM, Allard V, Andrieu B, Barot S, Enjalbert J, Gervais J, Goldringer I, Pommier T, Saint-Jean S, Le Roux X. 2020.** Plant functional trait variability and trait syndromes among wheat varieties: the footprint of artificial selection. *Journal of Experimental Botany* **72**: 1166–1180.
- Carmona CP, de Bello F, Azcárate FM, Mason NWH, Peco B. 2019.** Trait hierarchies and intraspecific variability drive competitive interactions in Mediterranean annual plants. *Journal of Ecology* **107**: 2078–2089.
- Chacón-Labela J, García Palacios P, Matesanz S, Schöb C, Milla R. 2019.** Plant domestication disrupts biodiversity effects across major crop types. *Ecology Letters* **22**: 1472–1482.
- Colombo M, Montazeaud G, Viader V, Ecartot M, Prosperi J-M, David J, Fort F, Violle C, Fréville H. 2022.** A genome-wide analysis suggests pleiotropic effects of Green Revolution genes on shade avoidance in wheat. *Evolutionary Applications* **15**: 1594–1604.

- Cunniff J, Wilkinson S, Charles M, Jones G, Rees M, Osborne CP. 2014.** Functional Traits Differ between Cereal Crop Progenitors and Other Wild Grasses Gathered in the Neolithic Fertile Crescent. *PLOS ONE* **9**: e87586.
- Dempewolf H, Baute G, Anderson J, Kilian B, Smith C, Guarino L. 2017.** Past and Future Use of Wild Relatives in Crop Breeding. *Crop Science* **57**: 1070–1082.
- Deng J-M, Li T, Wang G-X, Liu J, Yu Z-L, Zhao C-M, Ji M-F, Zhang Q, Liu J. 2008.** Trade-Offs between the Metabolic Rate and Population Density of Plants. *PLOS ONE* **3**: e1799.
- Deng J, Ran J, Wang Z, Fan Z, Wang G, Ji M, Liu J, Wang Y, Liu J, Brown JH. 2012a.** Models and tests of optimal density and maximal yield for crop plants. *Proceedings of the National Academy of Sciences* **109**: 15823–15828.
- Deng J, Zuo W, Wang Z, Fan Z, Ji M, Wang G, Ran J, Zhao C, Liu J, Niklas KJ, et al. 2012b.** Insights into plant size-density relationships from models and agricultural crops. *Proceedings of the National Academy of Sciences* **109**: 8600–8605.
- Denison RF. 2015.** Evolutionary tradeoffs as opportunities to improve yield potential. *Field Crops Research* **182**: 3–8.
- Denison RF, Kiers ET, West SA. 2003.** Darwinian Agriculture: When Can Humans Find Solutions Beyond the Reach of Natural Selection? *The Quarterly Review of Biology* **78**: 145–168.
- Des Marais DL, Hernandez KM, Juenger TE. 2013.** Genotype-by-Environment Interaction and Plasticity: Exploring Genomic Responses of Plants to the Abiotic Environment. *Annual Review of Ecology, Evolution, and Systematics* **44**: 5–29.
- DeWitt TJ, Sih A, Wilson DS. 1998.** Costs and limits of phenotypic plasticity. *Trends in Ecology & Evolution* **13**: 77–81.
- Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Colin Prentice I, et al. 2016.** The global spectrum of plant form and function. *Nature* **529**: 167–171.
- Donald CM. 1968.** The breeding of crop ideotypes. *Euphytica* **17**: 385–403.
- Donald CM, Hamblin J. 1976.** The Biological Yield and Harvest Index of Cereals as Agronomic and Plant Breeding Criteria. In: Brady NC, ed. *Advances in Agronomy*. Academic Press, 361–405.
- Egset CK, Hansen TF, Le Rouzic A, Bolstad GH, Rosenqvist G, Pélabon C. 2012.** Artificial selection on allometry: change in elevation but not slope. *Journal of Evolutionary Biology* **25**: 938–948.
- Eissenstat DM, Kucharski JM, Zadworny M, Adams TS, Koide RT. 2015.** Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest. *New Phytologist* **208**: 114–124.
- Enquist BJ, West GB, Charnov EL, Brown JH. 1999.** Allometric scaling of production and life-history variation in vascular plants. *Nature* **401**: 907–911.
- Finckh MR, Gacek ES, Goyeau H, Lannou C, Merz U, Mundt CC, Munk L, Nadziak J, Newton AC, de Vallavieille-Pope C, et al. 2000.** Cereal variety and species mixtures in practice, with emphasis on disease resistance. *Agronomie* **20**: 813–837.

- Fort F. 2023.** Grounding trait-based root functional ecology. *Functional Ecology*.
- Freckleton RP, Watkinson AR. 2001.** Asymmetric competition between plant species. *Functional Ecology* **15**: 615–623.
- Freschet GT, Pagès L, Iversen CM, Comas LH, Rewald B, Roumet C, Klimešová J, Zadworny M, Poorter H, Postma JA, et al. 2021.** A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. *New Phytologist* **232**: 973–1122.
- Fréville H, Montazeaud G, Forst E, David J, Papa R, Tenailon MI. 2022.** Shift in beneficial interactions during crop evolution. *Evolutionary Applications* **15**: 905–918.
- Fuller DQ. 2007.** Contrasting Patterns in Crop Domestication and Domestication Rates: Recent Archaeobotanical Insights from the Old World. *Annals of Botany* **100**: 903–924.
- Fuller DQ, Denham T, Arroyo-Kalin M, Lucas L, Stevens CJ, Qin L, Allaby RG, Purugganan MD. 2014.** Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record. *Proceedings of the National Academy of Sciences* **111**: 6147–6152.
- Gagliardi S, Martin AR, Filho E de MV, Rapidel B, Isaac ME. 2015.** Intraspecific leaf economic trait variation partially explains coffee performance across agroforestry management regimes. *Agriculture, Ecosystems & Environment* **200**: 151–160.
- Garland T, Downs CJ, Ives AR. 2022.** Trade-Offs (and Constraints) in Organismal Biology. *Physiological and Biochemical Zoology* **95**: 82–112.
- Garnier E, Navas M-L, Grigulis K. 2016.** *Plant Functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties*. Oxford, UK: Oxford University Press.
- Gaudet CL, Keddy PA. 1988.** A comparative approach to predicting competitive ability from plant traits. *Nature* **334**: 242–243.
- Getty T. 1996.** The Maintenance of Phenotypic Plasticity as a Signal Detection Problem. *The American Naturalist* **148**: 378–385.
- Glazier DS. 2022.** Variable metabolic scaling breaks the law: from ‘Newtonian’ to ‘Darwinian’ approaches. *Proceedings of the Royal Society B: Biological Sciences* **289**: 20221605.
- Glémin S, Bataillon T. 2009.** A comparative view of the evolution of grasses under domestication. *New Phytologist* **183**: 273–290.
- Gómez-Fernández A. 2023.** Plant size variation in crops: causes, mechanisms and consequences.
- Grime JP. 1977.** Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist* **111**: 1169–1194.
- Grossman JD, Rice KJ. 2012.** Evolution of root plasticity responses to variation in soil nutrient distribution and concentration. *Evolutionary Applications* **5**: 850–857.
- Hardin G. 1968.** The Tragedy of the Commons. *Science* **162**: 1243–1248.

- Harlan JR. 1967.** A wild wheat harvest in Turkey. *Archaeology* **20**: 197–201.
- Harlan JR, de Wet JMJ, Price EG. 1973.** Comparative Evolution of Cereals. *Evolution* **27**: 311–325.
- Harlan JR, de Wet JMJ, Stemler A. 1976.** Plant Domestication and Indigenous African Agriculture :453–464.
- Hay RKM. 1995.** Harvest index: a review of its use in plant breeding and crop physiology. *Annals of Applied Biology* **126**: 197–216.
- Hayes FJ, Buchanan SW, Coleman B, Gordon AM, Reich PB, Thevathasan NV, Wright IJ, Martin AR. 2019.** Intraspecific variation in soy across the leaf economics spectrum. *Annals of Botany* **123**: 107–120.
- Hector A. 1999.** Plant Diversity and Productivity Experiments in European Grasslands. *Science* **286**: 1123–1127.
- Hill CB, Li C. 2016.** Genetic Architecture of Flowering Phenology in Cereals and Opportunities for Crop Improvement. *Frontiers in Plant Science* **7**: 1906.
- Hodge A. 2004.** The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist* **162**: 9–24.
- Isaac ME, Martin AR, de Melo Virginio Filho E, Rapidel B, Roupsard O, Van den Meersche K. 2017.** Intraspecific Trait Variation and Coordination: Root and Leaf Economics Spectra in Coffee across Environmental Gradients. *Frontiers in Plant Science* **8**: 1196.
- Isaac ME, Nimmo V, Gaudin ACM, Leptin A, Schmidt JE, Kallenbach CM, Martin A, Entz M, Carkner M, Rajcan I, et al. 2021.** Crop Domestication, Root Trait Syndromes, and Soil Nutrient Acquisition in Organic Agroecosystems: A Systematic Review. *Frontiers in Sustainable Food Systems* **5**: 716480.
- Koehl MAR. 1996.** When does morphology matter? *Annual Review of Ecology and Systematics* **27**: 501–542.
- Kramer-Walter KR, Bellingham PJ, Millar TR, Smissen RD, Richardson SJ, Laughlin DC. 2016.** Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology* **104**: 1299–1310.
- Krouk G, Kiba T. 2020.** Nitrogen and Phosphorus interactions in plants: from agronomic to physiological and molecular insights. *Current Opinion in Plant Biology* **57**: 104–109.
- Kunstler G, Falster D, Coomes DA, Hui F, Kooyman RM, Laughlin DC, Poorter L, Vanderwel M, Vieilledent G, Wright SJ, et al. 2016.** Plant functional traits have globally consistent effects on competition. *Nature* **529**: 204–207.
- Ladizinsky G. 1975.** Collection of Wild Cereals in the Upper Jordan Valley. *Economic Botany* **29**: 264–267.
- Larson G, Piperno DR, Allaby RG, Purugganan MD, Andersson L, Arroyo-Kalin M, Barton L, Climer Vigueira C, Denham T, Dobney K, et al. 2014.** Current perspectives and the future of domestication studies. *Proceedings of the National Academy of Sciences* **111**: 6139–6146.

- Laughlin DC, Messier J. 2015.** Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends in Ecology & Evolution* **30**: 487–496.
- Lemoine T, Rimlinger A, Duminil J, Leclerc C, Labeyrie V, Tsogo M, Carrière SM. 2023.** Untangling Biocultural and Socioeconomical Drivers of African Plum Tree (*Dacryodes edulis*) Local Nomenclature Along a Rural-Urban Gradient in Central Cameroon. *Human Ecology* **51**: 721–736.
- Li B, Xu X, Zhang L, Han J, Bian C, Li G, Liu J, Jin L. 2020.** Above-ground biomass estimation and yield prediction in potato by using UAV-based RGB and hyperspectral imaging. *ISPRS Journal of Photogrammetry and Remote Sensing* **162**: 161–172.
- Litrice I, Violle C. 2015.** Diversity in Plant Breeding: A New Conceptual Framework. *Trends in Plant Science* **20**: 604–613.
- Loreau M. 1998.** Separating Sampling and Other Effects in Biodiversity Experiments. *Oikos* **82**: 600.
- Lynch J. 1995.** Root Architecture and Plant Productivity. *Plant Physiology* **109**: 7–13.
- Lynch JP. 2011.** Root Phenotypes for Enhanced Soil Exploration and Phosphorus Acquisition: Tools for Future Crops. *Plant Physiology* **156**: 1041–1049.
- Lynch JP. 2013.** Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. *Annals of Botany* **112**: 347–357.
- MacArthur R, Levins R. 1967.** The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *The American Naturalist* **101**: 377–385.
- MacLaren C, Waswa W, Aliyu KT, Claessens L, Mead A, Schöb C, Vanlauwe B, Storkey J. 2023.** Predicting intercrop competition, facilitation, and productivity from simple functional traits. *Field Crops Research* **297**: 108926.
- Marcelis LFM, Heuvelink E, Goudriaan J. 1998.** Modelling biomass production and yield of horticultural crops: a review. *Scientia Horticulturae* **74**: 83–111.
- Marshall M, Belgiu M, Boschetti M, Pepe M, Stein A, Nelson A. 2022.** Field-level crop yield estimation with PRISMA and Sentinel-2. *ISPRS Journal of Photogrammetry and Remote Sensing* **187**: 191–210.
- Martin AR, Rapidel B, Roupsard O, Van den Meersche K, de Melo Virginio Filho E, Barrios M, Isaac ME. 2017.** Intraspecific trait variation across multiple scales: the leaf economics spectrum in coffee. *Functional Ecology* **31**: 604–612.
- Martín-Robles N, Morente-López J, Freschet GT, Poorter H, Roumet C, Milla R. 2019.** Root traits of herbaceous crops: Pre-adaptation to cultivation or evolution under domestication? *Functional Ecology* **33**: 273–285.
- Meyer RS, DuVal AE, Jensen HR. 2012.** Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops. *New Phytologist* **196**: 29–48.
- Meyer RS, Purugganan MD. 2013.** Evolution of crop species: genetics of domestication and diversification. *Nature Reviews Genetics* **14**: 840–852.
- Milla R. 2023.** Phenotypic evolution of agricultural crops. *Functional Ecology* **37**: 976–988.

Milla R, Matesanz S. 2017. Growing larger with domestication: a matter of physiology, morphology or allocation? *Plant Biology* **19**: 475–483.

Milla R, Morente-López J, Alonso-Rodrigo JM, Martín-Robles N, Stuart Chapin F. 2014. Shifts and disruptions in resource-use trait syndromes during the evolution of herbaceous crops. *Proceedings of the Royal Society B: Biological Sciences* **281**: 20141429.

Milla, Osborne CP, Turcotte MM, Violle C. 2015. Plant domestication through an ecological lens. *Trends in Ecology & Evolution* **30**: 463–469.

Mommer L, Visser EJW, van Ruijven J, de Caluwe H, Pierik R, de Kroon H. 2011. Contrasting root behaviour in two grass species: a test of functionality in dynamic heterogeneous conditions. *Plant and Soil* **344**: 347–360.

Montazeaud G, Violle C, Fréville H, Luquet D, Ahmadi N, Courtois B, Bouhaba I, Fort F. 2018. Crop mixtures: does niche complementarity hold for belowground resources? An experimental test using rice genotypic pairs. *Plant and Soil* **424**: 187–202.

Montazeaud G, Violle C, Roumet P, Rocher A, Ecartot M, Compan F, Maillet G, Fort F, Fréville H. 2020. Multifaceted functional diversity for multifaceted crop yield: Towards ecological assembly rules for varietal mixtures. *Journal of Applied Ecology* **57**: 2285–2295.

Pélabon C, Firmat C, Bolstad GH, Voje KL, Houle D, Cassara J, Rouzic AL, Hansen TF. 2014. Evolution of morphological allometry. *Annals of the New York Academy of Sciences* **1320**: 58–75.

Pélissier R, Buendia L, Brousse A, Temple C, Ballini E, Fort F, Violle C, Morel J-B. 2021. Plant neighbour-modulated susceptibility to pathogens in intraspecific mixtures. *Journal of Experimental Botany* **72**: 6570–6580.

Peng JH, Sun D, Nevo E. 2011. Domestication evolution, genetics and genomics in wheat. *Molecular Breeding* **28**: 281–301.

Poorter H, Bühler J, Van Dusschoten D, Climent J, Postma JA. 2012. Pot size matters: a meta-analysis of the effects of rooting volume on plant growth. *Functional Plant Biology* **39**: 839.

Poorter H, Jagodzinski AM, Ruiz-Peinado R, Kuyah S, Luo Y, Oleksyn J, Usoltsev VA, Buckley TN, Reich PB, Sack L. 2015. How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytologist* **208**: 736–749.

Postma JA, Hecht VL, Hikosaka K, Nord EA, Pons TL, Poorter H. 2021. Dividing the pie: A quantitative review on plant density responses. *Plant, Cell & Environment* **44**: 1072–1094.

Preece C, Clamp NF, Warham G, Charles M, Rees M, Jones G, Osborne CP. 2018. Cereal progenitors differ in stand harvest characteristics from related wild grasses. *Journal of Ecology* **106**: 1286–1297.

Preece C, Livarda A, Wallace M, Martin G, Charles M, Christin P-A, Jones G, Rees M, Osborne CP. 2015. Were Fertile Crescent crop progenitors higher yielding than other wild species that were never domesticated? *New Phytologist* **207**: 905–913.

Prescott-Allen C, Prescott-Allen R. 1986. The first resource. *The first resource*.

- Prieto I, Litrico I, Violle C, Barre P. 2017.** Five species, many genotypes, broad phenotypic diversity: When agronomy meets functional ecology. *American Journal of Botany* **104**: 62–71.
- Prieto I, Violle C, Barre P, Durand J-L, Ghesquiere M, Litrico I. 2015.** Complementary effects of species and genetic diversity on productivity and stability of sown grasslands. *Nature Plants* **1**: 15033.
- Purugganan MD, Fuller DQ. 2009.** The nature of selection during plant domestication. *Nature* **457**: 843–848.
- Qin X, Weiner J, Qi L, Xiong Y, Li F. 2013.** Allometric analysis of the effects of density on reproductive allocation and Harvest Index in 6 varieties of wheat (*Triticum*). *Field Crops Research* **144**: 162–166.
- Reich PB. 2014.** The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**: 275–301.
- Reif JC, Zhang P, Dreisigacker S, Warburton ML, van Ginkel M, Hoisington D, Bohn M, Melchinger AE. 2005.** Wheat genetic diversity trends during domestication and breeding. *Theoretical and Applied Genetics* **110**: 859–864.
- Rolhauser AG, Windfeld E, Hanson S, Wittman H, Thoreau C, Lyon A, Isaac ME. 2022.** A trait–environment relationship approach to participatory plant breeding for organic agriculture. *The New Phytologist* **235**: 1018–1031.
- Roucou A. 2018.** Compromis écophysiologicals et contraintes biophysiques chez les céréales : impacts de la sélection agronomique et des conditions environnementales.
- Roucou A, Violle C, Fort F, Roumet P, Ecartot M, Vile D. 2018.** Shifts in plant functional strategies over the course of wheat domestication. *Journal of Applied Ecology* **55**: 25–37.
- Royo C, Álvaro F, Martos V, Ramdani A, Isidro J, Villegas D, García Del Moral LF. 2007.** Genetic changes in durum wheat yield components and associated traits in Italian and Spanish varieties during the 20th century. *Euphytica* **155**: 259–270.
- Royo C, Ammar K, Villegas D, Soriano JM. 2021.** Agronomic, Physiological and Genetic Changes Associated With Evolution, Migration and Modern Breeding in Durum Wheat. *Frontiers in Plant Science* **12**.
- Sadras VO, Lawson C, Sadras VO, Lawson C. 2011.** Genetic gain in yield and associated changes in phenotype, trait plasticity and competitive ability of South Australian wheat varieties released between 1958 and 2007. *Crop and Pasture Science* **62**: 533–549.
- Serrano L, Filella I, Peñuelas J. 2000.** Remote Sensing of Biomass and Yield of Winter Wheat under Different Nitrogen Supplies. *Crop Science* **40**: 723–731.
- Shipley B, De Bello F, Cornelissen JHC, Laliberté E, Laughlin DC, Reich PB. 2016.** Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia* **180**: 923–931.
- Sorrensen-Cothorn KA, Ford ED, Sprugel DG. 1993.** A Model of Competition Incorporating Plasticity through Modular Foliage and Crown Development. *Ecological Monographs* **63**: 277–304.
- Sultan SE. 2003.** Phenotypic plasticity in plants: a case study in ecological development. *Evolution and Development* **5**: 25–33.

- Tanno K, Willcox G. 2012.** Distinguishing wild and domestic wheat and barley spikelets from early Holocene sites in the Near East. *Vegetation History and Archaeobotany* **21**: 107–115.
- Tatsumi S, Loreau M. 2023.** Partitioning the biodiversity effects on productivity into density and size components. *Ecology Letters* **0**: 1–11.
- de Tombeur F, Lemoine T, Violle C, Fréville H, Thorne SJ, Hartley SE, Lambers H, Fort F. 2022.** Nitrogen availability and plant–plant interactions drive leaf silicon concentration in wheat genotypes. *Functional Ecology* **0**: 1–12.
- Vasseur F, Exposito-Alonso M, Ayala-Garay OJ, Wang G, Enquist BJ, Vile D, Violle C, Weigel D. 2018.** Adaptive diversification of growth allometry in the plant *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences* **115**: 3416–3421.
- Violle C, Garnier E, Lecoecur J, Roumet C, Podgeur C, Blanchard A, Navas M-L. 2009.** Competition, traits and resource depletion in plant communities. *Oecologia* **160**: 747–755.
- Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007.** Let the concept of trait be functional! *Oikos* **116**: 882–892.
- Voje KL, Hansen TF, Egset CK, Bolstad GH, Pélabon C. 2014.** Allometric constraints and the evolution of allometry. *Evolution* **68**: 866–885.
- Wainwright PC, Alfaro ME, Bolnick DI, Hulsey CD. 2005.** Many-to-One Mapping of Form to Function: A General Principle in Organismal Design?1. *Integrative and Comparative Biology* **45**: 256–262.
- Weigelt A, Mommer L, Andrzejek K, Iversen CM, Bergmann J, Bruelheide H, Fan Y, Freschet GT, Guerrero-Ramírez NR, Kattge J, et al. 2021.** An integrated framework of plant form and function: the belowground perspective. *New Phytologist* **232**: 42–59.
- Weiner J. 1990.** Asymmetric competition in plant populations. *Trends in Ecology & Evolution* **5**: 360–364.
- Weiner J. 2003.** Ecology – the science of agriculture in the 21st century. *The Journal of Agricultural Science* **141**: 371–377.
- Weiner J. 2004.** Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics* **6**: 207–215.
- Weiner J, Andersen SB, Wille WK-M, Griepentrog HW, Olsen JM. 2010.** Evolutionary Agroecology: the potential for cooperative, high density, weed-suppressing cereals. *Evolutionary Applications* **3**: 473–479.
- Weiner J, Freckleton RP. 2010.** Constant Final Yield. *Annual Review of Ecology, Evolution, and Systematics* **41**: 173–192.
- West GB, Brown JH. 2005.** The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization. *Journal of Experimental Biology* **208**: 1575–1592.
- West GB, Brown JH, Enquist BJ. 1997.** A General Model for the Origin of Allometric Scaling Laws in Biology. *Science* **276**: 122–126.

- West GB, Brown JH, Enquist BJ. 1999.** A general model for the structure and allometry of plant vascular systems. *Nature* **400**: 664–667.
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002.** Plant Ecological Strategies: Some Leading Dimensions of Variation Between Species. *Annual Review of Ecology and Systematics* **33**: 125–159.
- Westoby M, Jurado E, Leishman M. 1992.** Comparative evolutionary ecology of seed size. *Trends in Ecology & Evolution* **7**: 368–372.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, et al. 2004.** The worldwide leaf economics spectrum. *Nature* **428**: 821–827.
- Xiao S, Chen S-Y, Zhao L-Q, Wang G. 2006.** Density Effects on Plant Height Growth and Inequality in Sunflower Populations. *Journal of Integrative Plant Biology* **48**: 513–519.
- Xiong D, Flexas J. 2018.** Leaf economics spectrum in rice: leaf anatomical, biochemical, and physiological trait trade-offs. *Journal of Experimental Botany* **69**: 5599–5609.
- York LM, Nord E, Lynch J. 2013.** Integration of root phenes for soil resource acquisition. *Frontiers in Plant Science* **4**.
- Zeven AC. 1973.** Dr Th. H. Engelbrecht's views on the origin of cultivated plants. *Euphytica* **22**: 279–286.
- Zhang H, Mittal N, Leamy LJ, Barazani O, Song B-H. 2017.** Back into the wild—Apply untapped genetic diversity of wild relatives for crop improvement. *Evolutionary Applications* **10**: 5–24.



ANNEXES

Article S1.

Lemoine, T., Rimlinger, A., Duminil, J., Leclerc, C., Labeyrie, V., Tsogo, M., & Carrière, S. M. (2023). Untangling biocultural and socioeconomical drivers of african plum tree (*Dacryodes edulis*) local nomenclature along a rural-urban gradient in Central Cameroon. *Human Ecology*, 1-16.



Untangling Biocultural and Socioeconomical Drivers of African Plum Tree (*Dacryodes edulis*) Local Nomenclature Along a Rural-Urban Gradient in Central Cameroon

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Accepted: 21 June 2023 / Published online: 21 July 2023
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Abstract

In Cameroon, the African plum tree (*Dacryodes edulis* [G. Don] H. J. Lam) is widely cultivated for its fruits, which contribute significantly to household food security and economy. In order to analyze the links between the social and ecological systems that result in the remarkable fruit diversity, we focused on how the important varietal diversity of African plums was perceived and named by tree owners. We conducted semi-structured interviews in Center-Cameroon with 142 people belonging to the Beti ethnic group, in urban (Yaoundé), peri-urban and rural areas, and analyzed the data qualitatively and quantitatively. Along this urbanization gradient linking production to consumption regions, 158 different translated names were recorded. Most names (80%) were cited once, but some names based on fruit size and taste were common across the gradient. Although the highest total number of names was recorded in the rural site, many different names were also found along the urban–rural gradient. We did not detect difference in the number of named African plums between respondents with different characteristics. The local classification of African plums among the Beti was structured predominantly according to morphological and organoleptic criteria, but also to symbolic and practical criteria. African plums' names were based on people's fruit preferences, that favor large, oily, and blue to black fruits, and disregard pink-colored watery plums. This study is an entry point to explore the rising trade and thus ongoing domestication of the African plum tree from an often neglected perspective, that of local nomenclature.

Keywords Beti ethnic group · Central Africa · *Dacryodes edulis* · Domestication · Ethnobotany · Local nomenclature

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Introduction

In view of the variability among living organisms, people name diverse animal and plant species. Systems classifying this diversity can be formal and scientific with the aim of universal validity, or local. Local classifications, also called folk classifications, are intuitive and experience-based, forged by a group of individuals who create their own logic of grouping, specific to a given environment. Local classification of biodiversity within crop species leads to the definition of 'ethnovarieties'. These ethnovarieties or "farmer's varieties" arise from the recognition and naming of intraspecific diversity by local people (Karambiri et al., 2017; Rivera et al., 2006). The nomenclature scheme is defined by the number of ethnovarieties, which is itself the result of cultural heritage and selection (Stampella, 2016). It is a key element to understand the intraspecific diversity of a species, as it is the basis on which farmers select individuals, so that,

for each named type, their distinctive traits are preserved (Boster, 1985). Moreover, the number of ethnovarieties on which the nomenclature is based is affected by cultivation practices, which are themselves highly dependent on social, economic and cultural factors, and whose effect has rarely been considered (Adan et al., 2016).

Because local nomenclatures are based on phenotypic variations, they change throughout time, for instance to include new phenotypes and exclude those that have disappeared. Varietal names are not always consistent across regions, village communities or even within the same household (Appa Rao et al., 2002; Assogbadjo et al., 2008; Sambatti et al., 2001), and some varieties remain unnamed (Perales et al., 2003). The local nomenclature system is often based on the preference system of local communities (Mengue Efanden et al., 2003), with names being motivated, i.e., having an definite meaning. Local nomenclatures also result from two different dimensions of knowledge: theoretical knowledge, related to cognitive aspects (“I know the name of a variety, but I am not able to recognize or to describe it”), and practical knowledge, corresponding to the concrete application, skills and experience of this theoretical knowledge (“I know the name of a variety and I am able to recognize and describe it”) (Reyes-García et al., 2007). As a consequence, a diverse local nomenclature is indicative of the diversity of uses, preferences and practices, for instance of seed and seedling exchanges, of local populations.

Dacryodes edulis, commonly known as the African plum (Burseraceae family), is one of the most traded non-timber forest products (NTFP) in Central Africa. Although recent and accurate data of trade flows between Central African countries are lacking, African plums are among the five main NTFP crossing national borders in the region (Tabuna, 2007). Cameroon is the leader in African plum’s exportation, with hundreds of tons exported to Gabon, the Republic of Congo or Equatorial Guinea (Vunda, 2021). With its fruiting season extending over seven months of the year and its production alternating between north and south of the equator, it represents one of the most produced fruits in Central Africa, thus bringing a long-term source of food and income to local populations (Awono et al., 2002). The African plum is a major component of the Central African diet, notably in production regions where it is a staple food eaten roasted, boiled or dried and accompanied by cassava, corn or plantain (Tabuna & Tanoé, 2009). It is rich in lipids, proteins, vitamins, fatty acids and amino acids (Ajibesin, 2011; Tee et al., 2014) and can therefore be a significant source of energy for local populations. This emblematic Central African tree is mainly present in intertropical forest areas that offer favorable conditions for its cultivation, particularly in Southern Cameroon (Todou, 2015). It is abundant as an isolated tree in villages and in-home gardens, and as a

shade tree in cocoa- or coffee-based agroforestry systems (Schreckenberget al., 2002, 2006). A study by Jagoret et al. (2014) cites *D. edulis* as the only species found in all the cocoa farms inventoried in Central Cameroon. It is also one of the most common indigenous species in the urban area of Yaoundé (Mala, 2009).

The African plum shows a wide spectrum of diversity in terms of color, shape, size and taste (Anegbeh et al., 2005; Kengue et al., 2002; Leakey et al., 2002; Waruhiu et al., 2004). This phenotypic diversity can primarily be explained by the multiple selection pressures oriented by local agricultural practices (Leakey et al., 2002; Rimlinger et al., 2019), in conjunction with the allogamous reproductive system of the species (Kengue et al., 2002). Due to its highly traded fruits, the African plum tree has been well studied for breeding, domestication, cultivation and management aspects but there are still few studies about its local nomenclature system: the ones published refer to names given by different ethnic groups (Chevalier, 1949; Omonhinmin, 2012). Recently, it has been shown that the nomenclature used by three Cameroonian ethnic groups was highly varied for this species, especially for the Beti (Rimlinger, Duminil, et al., 2021). Beti indeed cited half of the names identified in this study (58% of the recorded local names), calling for a detailed account of the nomenclature for this group, and of the varieties that fall outside of it. There is also a need to recognize cultivators’ knowledge and preferences within the pool of varieties they maintain in their field; this is especially crucial in places integrated to commercial trade, as trade can focus on some phenotypes and hence prompt more selective dynamics. We address this by following one value chain of African plums in Central Cameroon, stretching from the urban consumption area of Yaoundé to the rural production area connected to it, and by considering the specific preferences associated with its trade.

The aim of this study is to describe the African plum nomenclature system and analyze its rationales and drivers. We do so among the Beti people, one Cameroonian ethnic group heavily involved in the cultivation of this species, and along an urbanization gradient including an urban, a peri-urban and a rural zone. Our first objective (1) is to explore the breadth of the local Beti nomenclature in each site including varieties that evade this nomenclature (unnamed varieties), and its links with socio-economic variables of African plum tree owners. Considering that traditional knowledge can vary with social characteristics and urbanization status of owners (Aswani et al., 2020; Gandolfo & Hanazaki, 2014), we specifically expect more varieties to be named in rural areas by older owners. Then, we further employ the classification scheme with the different classes of names observed, aiming at our second objective (2), to know how their distribution varies along the urbanization gradient. In our last objective (3), we

finally investigate the drivers of Beti local nomenclature in the light of its current trade, in particular through the fruit preference system.

We hypothesize that the weak selection of trees and seeds, as clonal reproduction is infrequent and cultivators keep trees even when they lack the right morphotype, the important networks of exchanges, and the allogamous reproduction system of this species favor a particularly rich nomenclature system in each site along the urbanization gradient (Rimlinger, Duminil, et al., 2021). We expect local varietal names to be linked to a range of motivations related to the organoleptic and morphological preference system of the fruit. Given the central place of Yaoundé in the African plum trade, we expected a majority of names motivated by the taste or the size of the fruit. Looking specifically at the distribution of those names along the gradient, we hypothesize that shared names reflect ongoing exchanges of information between Beti, which could illustrate the ubiquity and cultural significance of this species of fruit tree from rural to urban sites. Finally, we discuss the idea that the rich local nomenclature, because

of its diversity of names, can also be the reflection of an existing artificial selection and therefore of a domestication in progress.

Material and Methods

Study Site

This study was carried out with Beti people in the Centre region of Cameroon, along an urbanization gradient, composed of an urban, a peri-urban and a rural site (Fig. 1). People and languages classified as Beti (or Fang), pertaining to Bantu-speaking populations, are diversified. Beti language includes many dialects such as Bebele-Bebil or Bulu-Bene, which are mutually intelligible (Zamponi, 2009). As this study focuses on the region around the capital city of Yaoundé, mostly Eton and Ewondo were considered among Beti dialects. These locally dominant cultural linguistic groups were chosen because of their involvement in one of the major African plums value chains in Central Cameroon

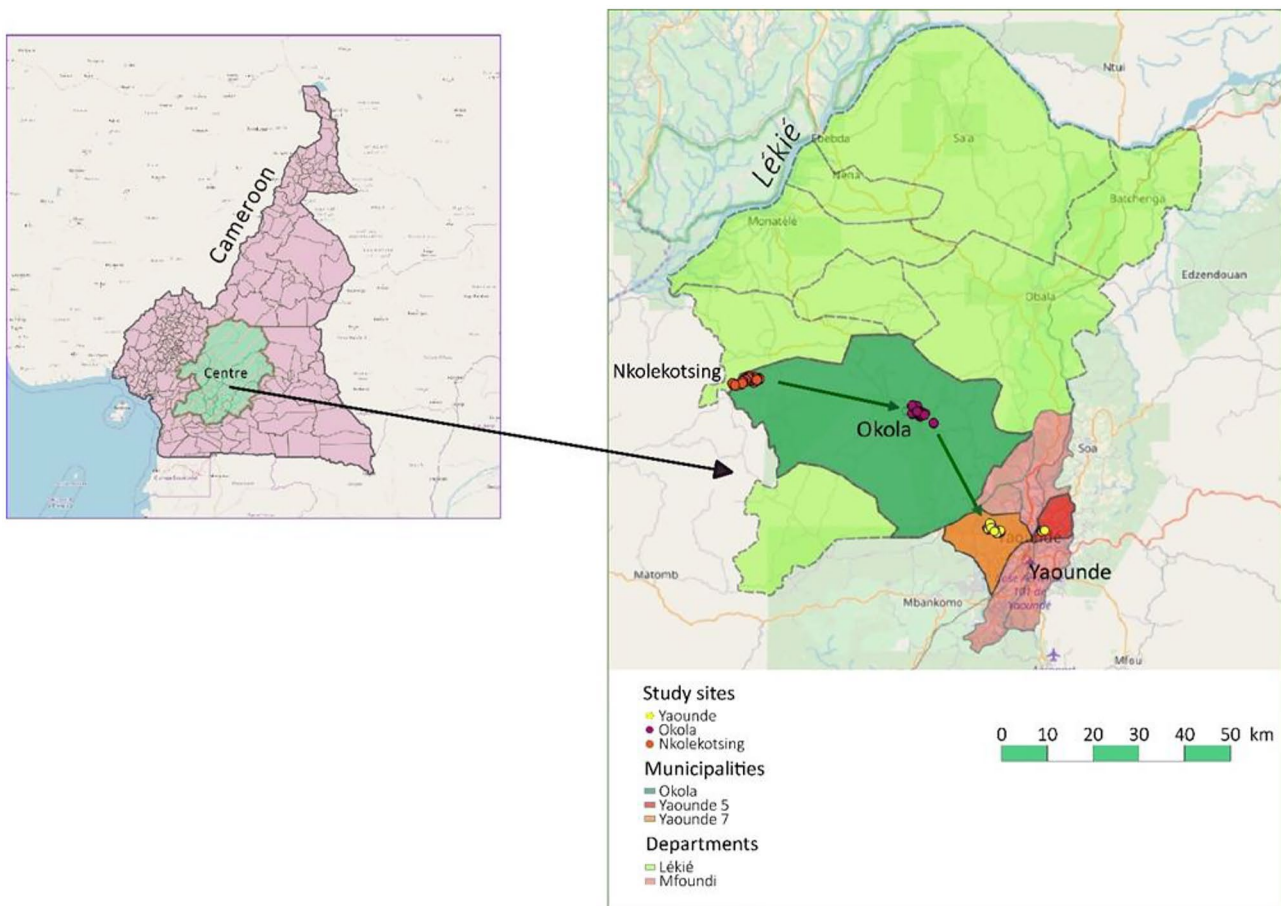


Fig. 1 Map illustrating the survey area along a city-countryside gradient in Cameroon. Study sites were precisely located at the following coordinates: Yaoundé ($3^{\circ} 52' 0.001''$ N $11^{\circ} 31' 0.001''$ E), Okola ($4^{\circ} 1' 0''$ N, $11^{\circ} 22' 60''$ E) and Nkolekotsing ($4^{\circ} 3' 36''$ N, $11^{\circ} 10' 48''$ E)

(Awono et al., 2002). The Eton are strongly represented in the Lékié department, North of the capital of Yaoundé (Van de Velde, 2008).

The three sites chosen along an urbanization gradient were: 1) the Oyom-Abang district in the Yaoundé city area (urban site); 2) the town of Okola, in the Yaoundé conurbation (peri-urban site); 3) the village of Nkolekotsing, in an isolated rural area chosen to be out of the direct influence of the city of Yaoundé, and especially out of the influence of the main road from Okola to Yaoundé (rural site; Fig. 1). Sites were chosen to ensure that Beti people were the majority group, in order to avoid a confounding effect between the ethnic group and the gradient.

A preliminary study of the African plum's value chains around the city of Yaoundé highlighted the main peri-urban areas involved in the production of plums that supply Yaoundé markets (Awono et al. in prep.). Among these areas, the rapidly expanding town of Okola is located in the Yaoundé conurbation, 32 km away from the city center. The peri-urban area was defined as being less than 50 km from Yaoundé and within the strong influence of the capital, with regard to its trade (Temple & Moustier, 2004): the city dwellers of Okola easily go to the capital for work or to sell their crops. Finally, the rural village of Nkolekotsing, 32 km away from Okola, was selected owing to its significant role in the cultivation of African plum trees, as informed by preliminary interviews in Okola. The majority of the 1500 inhabitants (census of 2018; MINEPAT & PDNP, 2018) of the village actively cultivates African plum trees and sells its different varieties.

Data Collection

In order to obtain collective and individual knowledge, we conducted several focus groups during four months of field work; 43 individual interviews in the urban site, 50 in the peri-urban site and 49 in the rural site. A consent form has been signed by all of the people surveyed.

Interviews focused on local nomenclature (the template used is provided as Supplementary Electronic Material 1). In general, plant local nomenclature is based on a series of well-known morphological descriptors, but also on

perceived descriptors, that are more labile or subjective (e.g. fruit taste; Boster, 1985).

In this study, we also pay attention to the knowledge gap, by considering the varieties that are known or observed but not (yet) named. To do so, we asked the respondents during individual interviews about the varieties of African plum trees they knew ('known' varieties) or had planted ('observed' varieties) on her/his property and about the detailed morphological and organoleptic description of their fruits (including fruit taste and texture; also see Rimlinger, Duminil, et al., 2021; Fig. S1 and Table S1), leading to six characteristics described by ethnovariety (fruit size, skin color, fruit shape, pulp color, texture and taste). We then asked for the names of these ethnovarieties (in Beti language and their translation in French), and these names could be known ('named' variety) or unknown ('unnamed' variety). Translations were carried out in French by the respondents themselves during most interviews, or sometimes by a third person (a relative). One of the researchers spoke Eton and could thus validate the proposed translations. Untranslatable (and thus unclassifiable by us) names were removed from the study. Additionally, questions targeted related knowledge about agricultural practices, fruit conservation, fruit preferences (desirable/undesirable fruit characteristics when buying an African plum fruit) and marketing of the African plums. For each interview, the respondent was questioned on his/her status (gender, age, family and residence status, ethnicity, main activity) and on the attributes of the household's fields (field size area, number of fruit tree species).

We chose people who owned at least one plum tree in their field or home garden as respondents and did so through a snowballing sampling. We conducted a total of 142 interviews with a balanced number of men and women (53% and 47% respectively), as well as seven focus groups in the three study sites. Focus groups aimed to present the researchers, the research project and its objectives to local populations in the different sites: although data collected during focus groups were not used per se, they helped understand the local context regarding history, cultivation, consumption and marketing of African plum in the different sites. The age of respondents ranged from 16 to 94 years old. The sample was relatively homogeneously distributed between age groups,

Table 1 Summary of the socio-economic characteristics of respondents as a percentage of the total for each category (age, gender) along the urbanization gradient. The Total line and column represent the total number (N) of respondents per socio-economic characteristic and site

Site	Age (years)				Gender		
	[0 ; 25]	[25 ; 50]	[50 ; 75]	[75 ; 100]	Men	Women	Total (N)
Urban	25	42	28	5	47	53	43
Peri-urban	28	42	24	6	60	40	50
Rural	27	45	24	4	51	49	49
Gradient	27	43	25	5	53	47	
Total (N)	38	61	36	7	75	67	142

with the dominant age group of respondents between 25 and 50 years old (Table 1). Most of the respondents in the peri-urban and rural sites were cultivators of fruit trees and market gardening crops, and sometimes went to sell them in Yaoundé or in local markets.

Local Nomenclature Classification

From the French translations of the names collected in the local language, the local names were classified into major naming classes, according to their linguistic motivation. All of the names that could not be translated by the respondents (12 local names) or that were too generic (e.g., the local name *sa'a* which only means “African plum”) weren’t considered. From the local names designating the ethnovarieties, we defined four naming classes of linguistic motivation: morphological, organoleptic, symbolic and topographic. Linguistic motivation of variety names does not concern the African plum variety as a biological object, but rather the way in which the names of varieties are linguistically constructed, by using either morphological, organoleptic, symbolic or topographic feature.

These four main classes of linguistic motivation were defined by us a posteriori to encompass the different types of motivation behind local names and were independent of the six morphological and organoleptic characteristics of varieties. For each ethnovariety, the descriptors (fruit size, skin color, pulp taste, ...) and their modalities (black color, white color, small size, large size, good or bad taste, i.e., sub-classes) were given by respondents and could be, or not, informative of local names. They were systematically collected in order for us to understand the logic of the local nomenclature.

Data Analysis

All data analyses were performed using the statistical software R version 3.6.1 (R Development Core Team, 2005). Following our hypothesis on the decrease in varieties named with younger age and proximity to urban center, the socio-economic characteristics of the respondents that could influence the number of African plum ethnovarieties named in the central region of Cameroon (objective 1) were analyzed using a Poisson regression model with a *glm* function from *stats* package. The dependent variable is the quantitative variable that counts named varieties for each person. The explanatory variables include the age, a continuous quantitative variable; the site, a categorical variable with three indicators; the average number of varieties observed and known per individual, which is a discrete quantitative variable. In order to obtain the most parsimonious model, we proceeded to the reduction of our model (forward selection) and thus chose the model with the lowest Akaike Information Criterion (AIC). A chi-square analysis was performed to establish whether there was a significant difference for the

respective proportions of local names given for each of the naming classes (morphological, organoleptic, symbolic and topographic) between sites along the gradient (objective 2).

To analyze the link between the six morphological and organoleptic characteristics of African plum varieties and the naming classes (morphological, topographic, etc.) in order to objectivate the preference system (objective 3), we carried out a multiple correspondence analysis (MCA), a method of factor analysis adapted to qualitative data. A three-dimensional space was obtained with the function *dudi.acm* from *ade4* package. The four naming classes (morphological, organoleptic, symbolic and topographic) were added as additional variables to analyze their association with the six morphological and organoleptic characteristics of African plum varieties, without a direct contribution to the MCA axis construction.

Based on consumer responses on their fruit purchase preferences (desirable or undesirable morphological and organoleptic fruit characteristics), we identified key descriptors (fruit size, skin color, pulp taste,...) and sub-classes (black color, white color, small size,...) predicting purchase that may constitute motivations in the nomenclature of African plum and explains the dominance of some descriptors in local nomenclature (objective 3). The decision tree (DT) designed in the present study was based on the standard CART algorithm build with the function *rpart* from the package *rpart* (Therneau et al., 2013). The DT is a tree-like structure, where each internal node denotes a test on an attribute, each branch represents conjunctions of input features that resulted in those outcomes of the test, and each leaf node (terminal node) holds a class label. The two classes are fruit purchase (1) or rejection of fruit purchase (0).

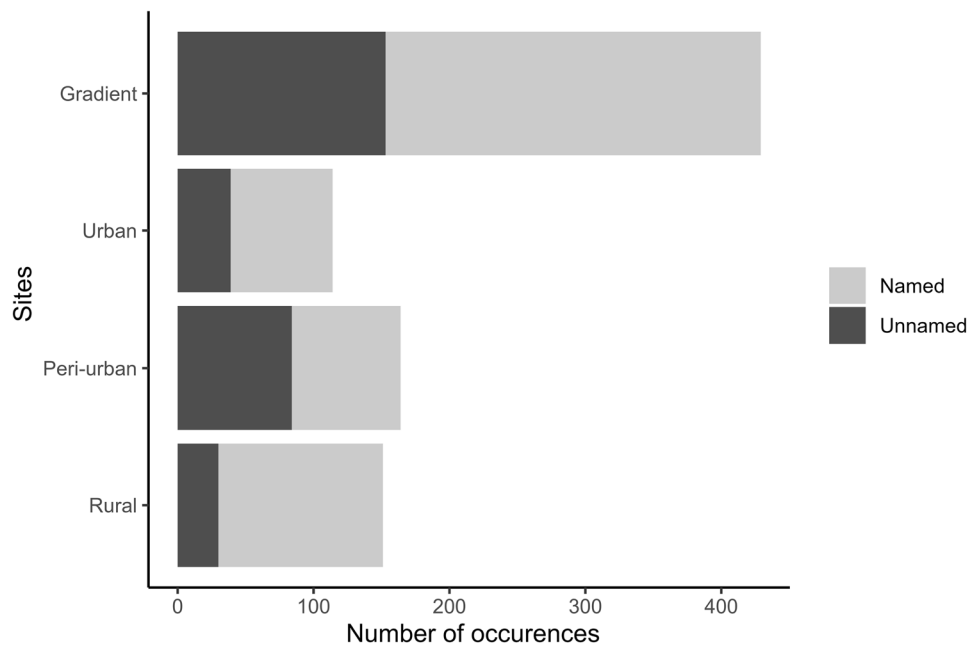
Results

Beti African Plum Nomenclature: A Diversity of Local Names

Named and Unnamed Varieties Along the Gradient

At the species level, the people interviewed commonly refer to the species *D. edulis* as either “prunier” in French or “sa” in Beti. At the intraspecific level, a total of 173 different local names (ethnovarieties with a Beti origin, whether translated or not) were cited along the gradient (out of a total of 276 local names collected; Fig. 2 and Table S1). They were cited during interviews at home, based on memories (both from “known” and “observed” varieties). Local names were recorded in all sites along the gradient. Rural site had the highest total number of names, with 79 different names of which 16 were cited twice or more (a cited total of 121 names). It was followed by the peri-urban site,

Fig. 2 Number of named and unnamed Beti varieties along the gradient, both from “known” and “observed” varieties



with 53 different names of which 13 were cited multiple times (80 names in total) and the urban site, with 59 different names of which 7 were cited multiple times (75 names in total). Higher numbers of unnamed varieties (both from “known” and “observed” varieties) were mostly recorded in the peri-urban site (84 varieties) and urban (39 varieties) site whereas only 30 unnamed varieties were found in the rural site (Fig. 2; see Table S2 for the number of named and unnamed in observed or known varieties according to the socio-economic variables).

Named and Unnamed Varieties According to the Socio-Economic Variables

Age, gender and farming activity did not provide additional information to explain the average number of African plums named and were therefore excluded through the model selection method. The site had a significant effect ($p < 0.001$; Table S3) on the average number of African plums named per person with an alpha risk of 5%. In both the peri-urban and in the urban site, there were fewer named varieties on average per individual compared to the rural site (Tukey method: $p < 0.001$). Additionally, we found a significant association ($p < 0.001$; Table S3) between the average number of “observed” and “known” varieties per individual and the average number of African plums named per person with an alpha risk of 5%. On average, “observed” varieties were less named than “known” varieties per individual in our gradient.

Local African Plum Classification Scheme

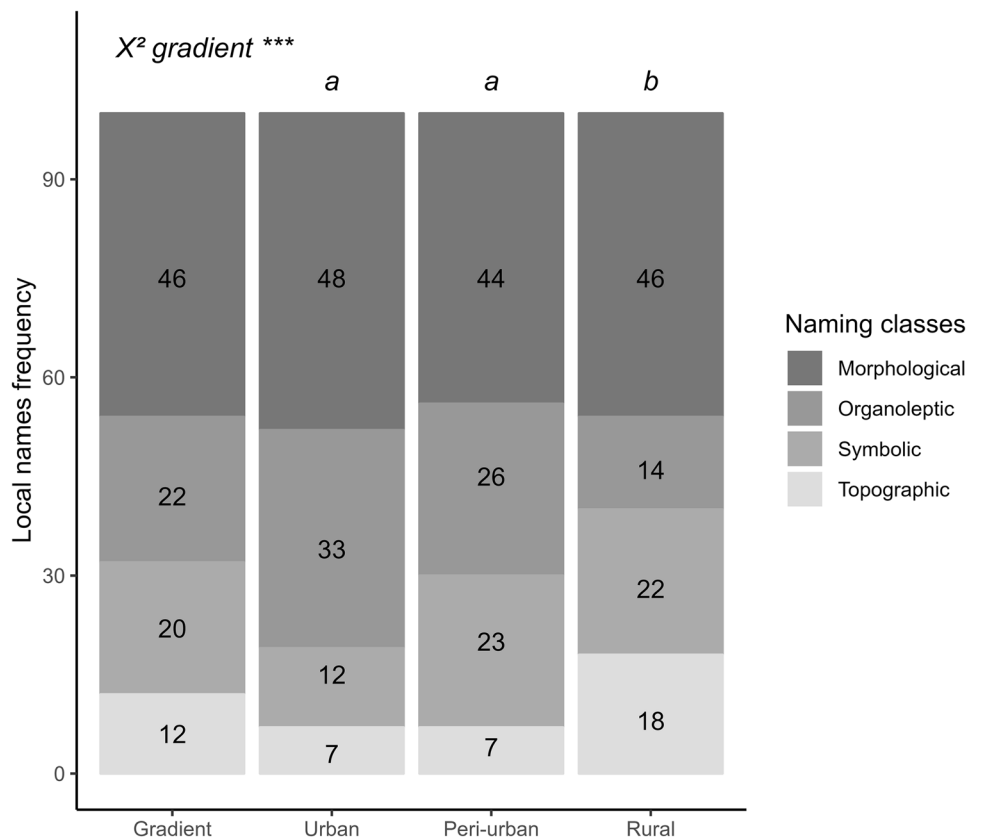
Naming Class and Characteristics Used by Beti People

Across the gradient, a total of 158 translated different local names were listed at least once. The collected names of ethnovarieties were related to one of the four naming classes or linguistic motivations considered (Table 2; for the exhaustive list of variety names see Table S1): (1) morphological (fruit size, shape, color of skin and pulp, pulp thickness; 46%), which can be illustrated, for example, by the name of *apouma sa'a* meaning ‘white plum’, (2) organoleptic (fruit taste and smell, oily or watery texture of the pulp; 23%), such as the name *bissono*, which translates to ‘tears’, suggesting the fruit’s extreme sourness; (3) symbolic (linked to the family or tree’s history, linked to a special event of the tree or the people, metaphoric name of cultivators or the trees; 20%), like the name *ntongo benui* meaning ‘the foster mother’; and (4) topographic (characteristics of the environment in which the plum tree is planted, or its geographic description; 12%), for instance, the name *zang i keukeu* designating the ‘middle of the cocoa farm’ and *milo’midouk*, translated as ‘toilet fly’, referring to the place where the waste is put, often located at the back of the kitchen, between the house and the cocoa farm. The first three naming classes are further broken down into different sub-classes, whereas the topographic class is not (Table 2).

Table 2 Local classification of naming classes, cultivators' descriptors and sub-class examples. The frequency per descriptor corresponds to the descriptor's proportion among all the names along the gradient. The frequency of sub-class corresponds to the sub-class proportion among the naming classes. To characterize these naming classes, we only worked with names that had a translation

Naming class	Descriptor	Frequency (%)	Sub-class	Frequency (%)
Morphological	Fruit size	29.7	Large fruit	40
			Small fruit	24
	Fruit shape	6.6	Long fruit	9
			Short fruit	2.5
			Original fruit	2.5
			Special skin	2
	Skin colour	5.8	White skin	7.6
			Black skin	2
			Mottled skin	2
			Special skin	2
Pulp colour			2.7	Red pulp
Organoleptic	Pulp thickness	1	Green pulp	0.8
			Fleshly pulp	2.5
	Fruit taste	17	Good fruit	34.5
			Sour fruit	41.4
	Pulp texture	5	Watery pulp	3.5
			Oily pulp	17
			Fruit smell	0.8
Symbolic	19.7	History	35	
		Planter's name	28	
		Name of a third party	37	
Topographic	Environment	12		

Fig. 3 Proportion of local names for the entire dataset and for each site individually. The results of the chi-squared test are represented by letters (sites sharing the same letter indicate no significant differences). $p < 0.05$ *, ** $p < 0.01$; *** $p < 0.001$. The X^2 gradient corresponds to differences in naming classes along the gradient



Naming Classes, Descriptors and Sub-Classes Along the Gradient

Significant differences were observed in the respective proportions of local names given to each naming class (morphological, organoleptic, symbolic and topographic, Fig. 3) between urban site and rural site (X^2 ; $p < 0.01$) and peri-urban site and rural site (X^2 ; $p < 0.05$). Overall, along the gradient, there was a significant difference between the different proportions of naming classes cited (X^2 ; $p < 0.001$).

The morphological naming class was consistently the most significant naming class along the gradient, but it was higher in the urban site (48% of varieties), than in rural and peri-urban sites (Fig. 3). Among the respondents, 46% cited at least one name that included morphological features. Some morphological features such as fruit size and skin color, which respectively had two and four sub-classes, were frequently used, accounting for 29.7% and 5.8% of all the names. Other features were less commonly used to motivate the variety names (such as pulp thickness, 1%; Table 2). Compared to the morphological naming class, the organoleptic naming class was less frequently used to motivate the variety names along the gradient (22%). Varieties' names were mainly motivated according to fruit taste (17%). The organoleptic naming class was predominantly used in the urban site, with 33% of local names construction based on organoleptic features while it was less represented in the rural site (14%) (Fig. 3). The symbolic naming class accounted for 19.7% of the listed names (Table 2). The most important symbolic sub-classes referred to names of people (13% of all the names) and to the personal history of the people interviewed (i.e., themselves, their family, or their family tree, 7% of all the names). This personal history sub-class was mainly represented in the peri-urban site, with 14% of total peri-urban names, whereas it accounted for only 4%

of the total in the urban site (Fig. 3). The topographic naming class corresponded to 11% of the names (Fig. 3). This naming class was mainly used in the rural site (17% of local names) while it was marginally used in the urban (7%) or peri-urban site (7%).

Redundancy of Local Names Along the Gradient

A high proportion (80%) of local names were cited only once. However, the occurrence of citations within each site varied, ranging from one to 23 citations; the highest number was recorded in the rural site for *leboack*, a morphological name meaning 'squash' (Table 3). This ethnovariety corresponded to a large and oily plum, that was reported to be particularly tasteful. Some of these local variety names were not only present in a single site but were shared between sites (7.6% of the total different local names along the gradient). Seven local variety names were shared between two sites: four were shared between the peri-urban and the rural sites, one was shared between the urban and the rural sites, two were shared between the urban and the peri-urban sites. Five ethnovarieties were named in all three sites: *leboack*, accounted for 9% of citations along the gradient, *mononome* (5.7%), *saang* (3.4%), *lebin ntomo* (2.7%) and *midjono* (1.1%).

Conceptualizing the Local Nomenclature Scheme

The naming of cultivated varieties is influenced by dynamic and contemporary social processes, involving the exchange of seeds, their names, and other associated information. Due to the nutritional value and extensive phenotypic diversity of African plums in terms of shape, color, size and taste, local nomenclature is based on various fruit morphological and organoleptic features. These criteria enable people to name

Table 3 Local names shared between two or three sites along the gradient, their naming class, translation, and percentage of citations among the set of local names collected along the gradient and translated

African plum's name	Translation	Naming class	Sites where the variety name was collected	Citation (%)
<i>Abeng</i>	The beauty	Organoleptic/ Morphologic	Peri-urban/Urban	1.9
<i>Avieu levong</i>	Red fat	Morphologic	Peri-urban/Urban	0.8
<i>Ayap sa'a</i>	The long plum	Morphologic	Peri-urban/Urban	0.8
<i>Ikoum ibey</i>	A short "ibey" tree trunk	Topographic	Rural/Urban	1.1
<i>Itobo</i>	The big plum	Morphologic	Peri-urban/Urban	2.3
<i>Lebin ntomo</i>	Sheep's testicles	Morphologic	Rural/Peri-urban/Urban	2.7
<i>Leboack</i>	Gourd	Morphologic	Rural/Peri-urban/Urban	9
<i>Midjono</i>	The tears	Organoleptic	Rural/Peri-urban/Urban	1.1
<i>Mintongo</i>	The long plum	Morphologic	Peri-urban/Urban	2.7
<i>Mononome</i>	The bird's plum	Morphologic	Rural/Peri-urban/Urban	5.7
<i>Parla</i>	Behind the house	Topographic	Peri-urban/Urban	0.8
<i>Saang</i>	The sour fruit	Organoleptic	Rural/Peri-urban/Urban	3.4

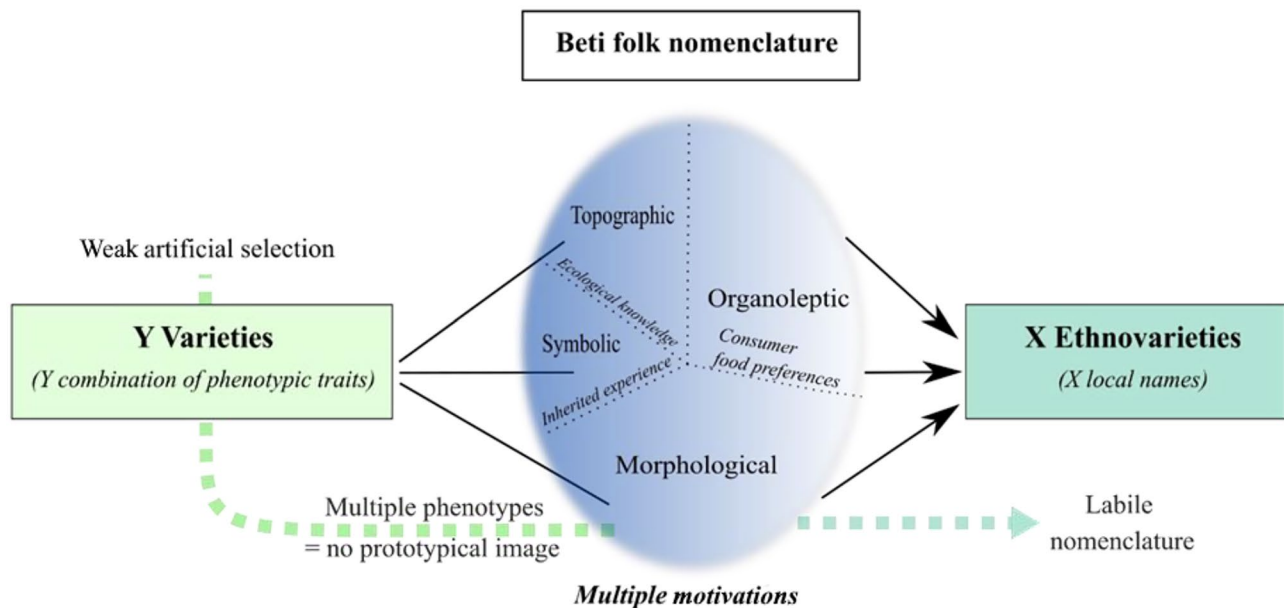


Fig. 4 General diagram (the size of each pie fraction is not scaled) illustrating the different criteria involved in naming the African plum among the Beti people and the relationship between domestication and local nomenclature. The phenotypic variation of African plums,

resulting from a weak artificial selection, leads to a proliferation of names, making it challenging to establish a consensus in nomenclature

and distinguish between different types and tastes of fruit within this wide range of perceived fruit variability (Fig. 4).

The Food Preference System: Driver of African Plum Nomenclature

African Plum Varieties' Characteristics and Correspondences with Naming Classes: Fruit Quality Indicators

The MCA, used to see the links between the different morphological and organoleptic characteristics of African plums, had its first two axes representing 24.9% of the total variance (Fig. 5).

The maximum contributions for the first axis were observed for the characteristics of watery pulp texture (22.6%), bad taste (19%), red pulp color (14%) and pink skin color (6%). The first axis effectively distinguished between plums with good taste on the left and plums with bad taste on the right. Characteristics associated with bad taste included pink skin color, red flesh color, and a high-water content. For the second axis, the maximum contributions were observed for the characteristics of spherical shape (26%), small size (23%), dry pulp texture (12.7%) and large size (10%). The second axis effectively differentiated between large plums at the top and small plums at the bottom. The morphological, topographic, and symbolic naming classes were located close to each other in the center of the space. The morphological and topographic naming classes

were closer to the center and characterized by good-tasting plums with blue skin color, white flesh color and medium size. Ethnovariety names related to symbolic naming class, in the center of the graph, were not associated to specific morphological or organoleptic fruit characteristics. Ethnovariety names related to organoleptic criteria appeared to be linked to large average-tasting plum with a conical shape and a violet or two-colored skin. The variety names provided characteristic information that represents the quality of the fruits which influences the decision to purchase or not.

Purchase Preferred Characteristics

Among the 16 potential predictors, the decision tree identified four descriptors and eight sub-classes as key criteria in predicting purchase behavior: fruit taste (tasty/sour), fruit size (large), skin color (blue, pink, white, black), and pulp texture (oily pulp) (Fig. 6). The CART decision tree achieved a correct prediction of purchase or rejection in 88.4% of cases in the training datasets and 87% in the test datasets (cross-validation). The decision tree determined that all interviewed individuals, except one would buy a tasty fruit. Furthermore, if the fruit was both tasty and large, ten people would purchase it. Similarly, if the fruit had skin color other than pink (white, blue or black) and was considered oily in texture, it would be purchased by 104 individuals. The three most important morphological characteristics for fruit rejection were bad taste, followed by small size and pink skin color.

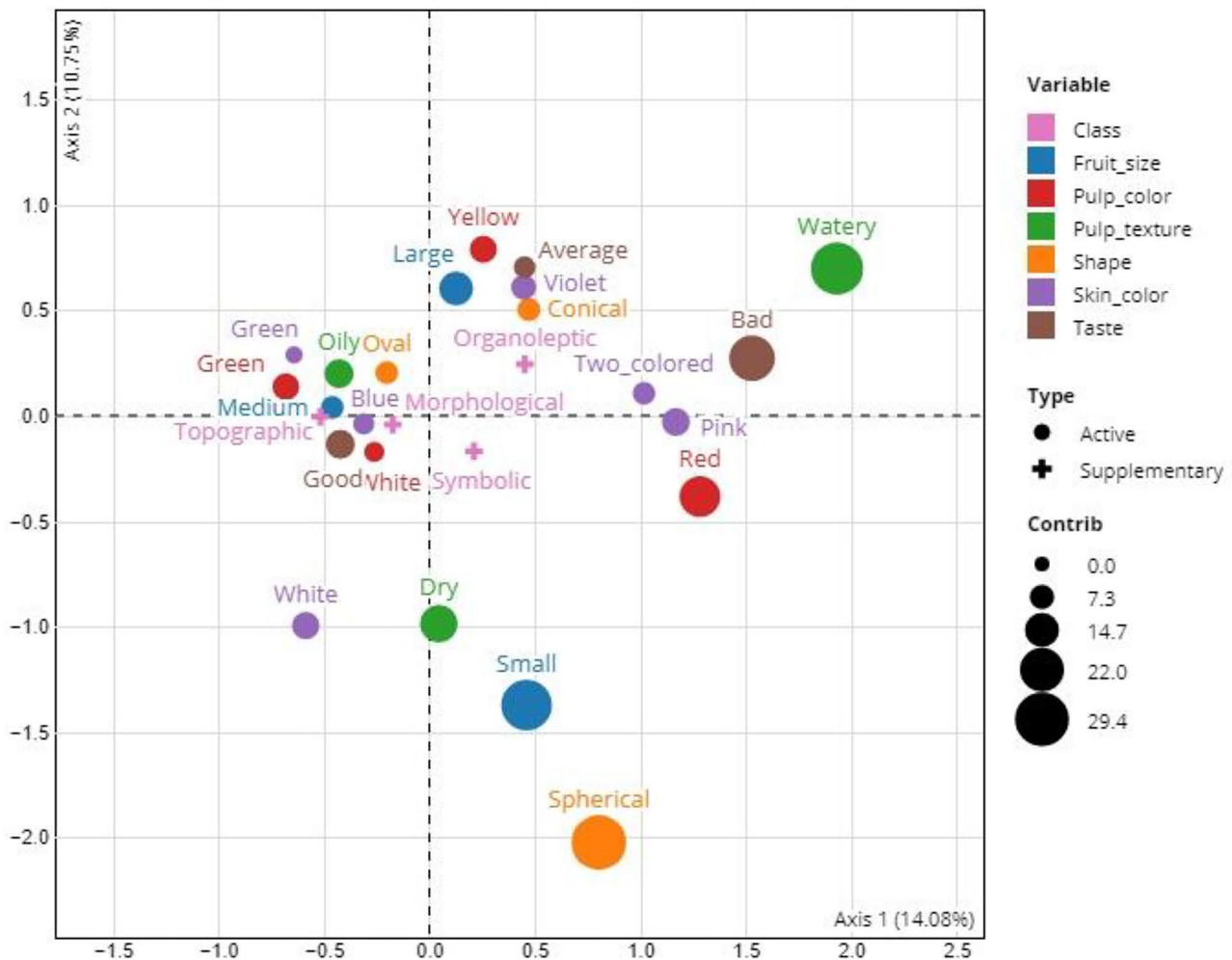


Fig. 5 Multiple correspondence analysis (MCA) based on six morphological and organoleptic characteristics of African plum varieties namely fruit size, skin color, shape, pulp color, texture and taste. The ethnovariety naming classes (morphological, organoleptic, symbolic

and topographic) are represented as an additional variable (highlighted in pink color and labeled as supplementary type). The size of each circle corresponds to the contribution of the respective variable to the inertia along each axis

Discussion

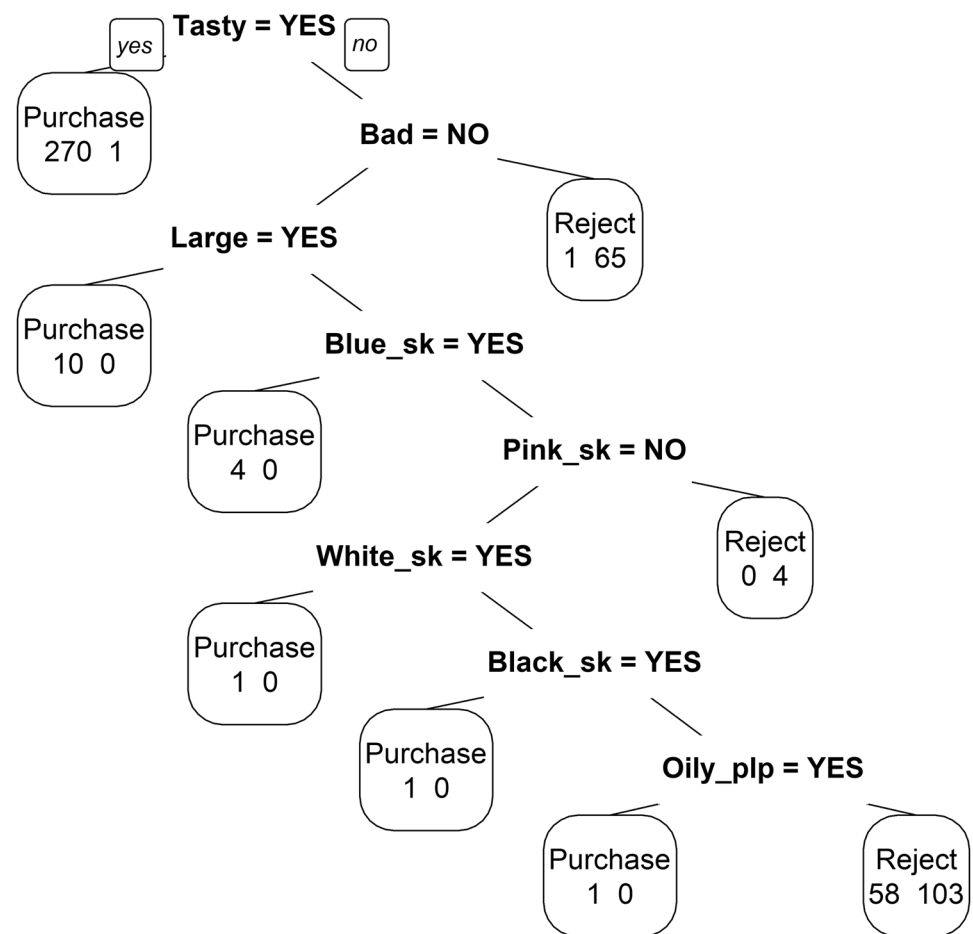
In this study, through surveys of 142 Beti people along an urbanization gradient in Cameroon, we uncovered a rich local nomenclature for the African plum. After recording these numerous names, we aimed to understand the underlying logic and motivations behind its nomenclature. Our findings revealed a rich diversity of 158 ethnovarieties of African plum, identified across rural, peri-urban and urban sites. The cultural importance of this fruit tree species but also the booming demand linked to the trade and consumption of African plum have been identified as major drivers of the richness of local names and of the logic of this nomenclature. Lastly, the linguistic diversity and the phenotypic diversity of the African plum are mutually related and assessing the status of each of these diversities in relation to the others can constitute a means of evaluating the selection pressures on fruit tree.

Local African Plum Nomenclature Rooted in Cameroonian Territories and Beti Knowledge

In the Center region of Cameroon, our study revealed an exceptional richness in local nomenclature for the African plum, among the Beti people. We documented a total of 158 different local names, including both known and observed varieties (with a French translation), along the urban, peri-urban, and rural gradient. Such diversity in local names within a single ethnic group is quite remarkable, as previous studies demonstrating a such richness typically involve regions with a mix of cultural and linguistic groups (Agbo et al., 2020; Assogbadjo et al., 2008; Gwali et al., 2011; Jianchu et al., 2001; Mekbib, 2007).

This study observed that people were able to cite names of both observed and known varieties, indicating the widespread presence and cultural significance of the African

Fig. 6 Decision tree model, which displays the hierarchy of splits with eight branch nodes and nine leaf nodes based on eight characteristics. A total of 16 descriptors were used to build the tree. The label “Reject” corresponds to the rejection of fruit purchase (0), and the label “Purchase” corresponds to fruit purchase (1). Sk = skin; plp = pulp. For each label, if it is a rejection label (on the right side of the decision tree), the first number corresponds to the count for rejection and the second for non-rejection, if it is a purchase label (on the left side), the first number corresponds to the count for purchase and the second for non-purchase



plum across rural to urban sites. The Beti nomenclature encompassed a wealth of known varieties collected in this study (150 in total), that represented both theoretical and practical knowledge acquired over time (Reyes-García et al., 2007). Respondents spontaneously described known varieties that came from their village and that held special significance in their childhood, or possessed distinct and remarkable characteristics, such as highly sour, delicious, large, dark and shiny fruits. These aspects were reflected for instance by the ethnovariety *modza*, translated by the “village chief”, which had a distinct shape, and evoked specific childhood memories in the respondent. Local names have persisted in the individual and collective memory, demonstrating their long-lasting nature.

In our study, the urban site had the highest number of known varieties, despite the limited availability of land for planting within the city. African plum trees still found a place in family compounds, with city dwellers planting a few trees, that held great significance as they represented “a piece of the village that they keep close to them”. This connection between rural and urban environments in Cameroon (Mainet, 2017) facilitated the transmission

and perpetuation of traditional ecological knowledge and practices.

The overall richness of ethnovarieties was significant across the entire gradient, but it was the greatest in the rural site, especially concerning observed varieties. Although the rural site is more isolated, virilocality, a social rule of marriage among the Eton, leads to the mandatory establishment of women in their husband’s native village. As their move to their husband’s village, women bring both their own knowledge on fruit growing practices, but also African plum names and varieties they are familiar with. For example, Mrs. M. C. shared that “when she came in marriage, she told her husband that she wanted to eat *leboack*, her father’s plum in the village”. This indicates that women may therefore be one of the drivers of the known and observed varietal diversity of the rural site, as observed for other crops in Central Africa (Delêtre et al., 2011).

Variety exchanges also allow names and information about their characteristics to be exchanged. In Cameroon, seeds from African plums are disseminated through four main channels: gifting between individuals; purchasing at markets or in nurseries; transporting varieties during family visits to

villages; spontaneous propagation (Schreckenberget al., 2002). Seed exchange is one of the drivers of the diversity of local names of our sites, as was also observed in other studies in France or Kenya (Labeyrie et al., 2019; Thomas et al., 2011), and contributes to the genetic diversity of the species, enriching the genetic pool in Yaoundé (Rimlinger, Avana, et al., 2021). Seed circulation systems operate openly within and between sites, which likely accounts for the widespread dissemination of names in both urban and rural sites. In fact, seed commercial circulation further accentuates this process, as each of our sites is connected to the African plum trade.

Respondents from the rural site named more ethnovarieties compared to other sites along the gradient. This can be attributed to the strong interest to the cultivation of African plum trees among rural dwellers in Centre Cameroon. Species cultivation and the richness of its nomenclature can thus be positively linked, as shown for other tree species (Adan et al., 2016). However, there seems to be a tipping point in this relationship: in our study, the peri-urban site had the highest proportion of unnamed varieties accounting for 52% of the total, in contrast to 20% in the rural site. This site, characterized as a secondary city experiencing rapid population growth and serving as an important hub for African plum production, exemplifies how the dynamic development of economic rationality can trigger significant cultural and symbolic changes. Interestingly, only in the peri-urban site did people explain that they saw no purpose in naming their trees, and instead, children were the ones assigning names.

Overall, the “known and observed” diversity of varietal names for the African plum reflects the collective contributions of individuals who assign names based on the fruits they grow, remember, bring, or exchange. While people acquire knowledge of variety names from others, it is not uncommon for names to be reassigned. This occurs when farmers observe significant phenotypic differences that are distinctive enough to warrant a separate name for a given morphotype. The complexity of the nomenclature is further influenced by the fact that the same phenotypic difference may carry different weight or significance for different farmers (Sambatti et al., 2001). The multitude of names reflects the diverse perception of fruit morphotypes and other characteristics associated with the species (Boster, 1985). Regarding economic integration and urbanization, they have been shown to have adverse effects on traditional knowledge (Gandolfo & Hanazaki, 2014). However, in the case of African plum, the exchange of varieties helps counterbalance these effects, contributing to the maintenance and preservation of traditional knowledge despite economic and urban influences (Agbo et al., 2020; Assogbadjo et al., 2008; Godoy et al., 2005; Nuijten & Almekinders, 2008; Sogbohossou et al., 2014).

This study reveals that the number of named African plum varieties is consistent across different socio-economic

categories of respondents, irrespective of age or gender. This finding underscores the shared cultural significance of the tree within the community. Despite the influence of urbanization and other factors, the local nomenclature remains deeply ingrained in Cameroonian territories, including among the younger generation. It is worth noting that the Beti nomenclature does not revolve around specific local names for African plum ethnovarieties but rather follows a consensus-based nomenclatural rationale embraced by the respondents.

Local African Plum Nomenclature Scheme

Local nomenclatures are often based on culinary, medicinal or agronomic uses (growth, resistance to climatic conditions, cultivation), as well as domestication or selection practices (Appa Rao et al., 2002), and on origin/site characteristics where species or varieties developed (Loko et al., 2018; Sathya, 2014). When it comes to African plum, no names specifically referring to fruit uses, tree care or growth patterns were found. Interestingly, a significant proportion of African plum names, particularly in the rural site, consisted of toponyms associated with the site’s history and environmental criteria. These toponyms serve the purpose of distinguishing male trees or common/average African plums, which typically exhibit traits such as a blue color, medium size, and good taste. These toponyms reflecting ecological, agronomic, and historical knowledge of the cultivators can also be replaced, after fruit production, by a name related to morphological or organoleptic characteristics after the fruits have been produced.

Local nomenclature is also influenced by cultural criteria (Appa Rao et al., 2002; Nuijten & Almekinders, 2008). In the rural site, the naming of African plums’ trees reflects memorial and symbolic values. Cultivators have the option to name a tree after themselves or after significant individuals as a way to honor and remember them. For instance, a tree named ‘*avita sia*’ translated as “the uprooted who has risen again” symbolically represents a woman’s triumph over a serious illness during the time she planted the plum tree. “Symbolic” nomenclature, involving the names of individuals, is more commonly used for known varieties, while observed varieties tend to be associated with memories of a person’s life, leading for instance to a higher prevalence of names related to topography.

Symbolic names often highlight remarkable size, color and/or shape descriptors, such as the white-skinned plums, which are described as “rare”, “not sold on the market”, “prestigious”, “for family”. Other symbolic references are found for African plum nomenclature. For instance, the ‘*ntongo benui*’ tree (“food for orphans”) refers to the very large quantities of fruit produced by this variety which can be shared with the community. These “symbolic” nicknames effectively convey fruit or tree characteristics through shared

analogies or metaphors connected to the community's history and everyday life experiences.

Overall, the local names of African plums bear witness to the multiple interactions between tree owners and their trees. They manifest how, over time, biological and cultural diversity have become linked: the diversity of African plums is now encoded by *Beti* values, practices, and memories.

Market Impact on African Plum Nomenclature

The naming diversity of African plums is indicative of people's fruit perceptions, but also preferences, as observed in other African tree species (Assogbadjo et al., 2008; Ekué et al., 2010). As individual preferences for fruits can vary depending on whether the fruit is intended for self-consumption or the market, varietal names also aid in recognizing preferred fruits and subsequently influence decisions related to harvesting or purchasing. This might explain the high number of local names related to organoleptic features in the urban site, where individuals primarily act as consumers. When purchasing plums from the market, fruit taste appears to be the most significant criterion. The proportion of oil or water in the fruit pulp is also a notable characteristic that is identifiable and named, as it is of interest to consumers. Size and color, which can serve as indicators of fruit quality, are informative visual and naming criteria. Market consumers tend to gravitate towards large, oily, dark, and blue-to-black fruits, while disregarding pink-colored watery plums. While taste remains the primary criterion, size become less important if the plum is small but flavorful. On the other hand, large plums with average (slightly acidic) or even very sour taste still attract consumers. Size, taste and color (as a proxy for taste), which are criteria of interest for sale, significantly impact the price of plums (Anegbeh et al., 2005). Thus, local nomenclature is closely connected to management practices, cultivation techniques, and tree selection that align with both self-consumption and consumer food preferences.

The Labile African Plum Names: Domestication Processes Underway

African plum local nomenclature naming is a dynamic and evolving process which results from weak breeding selection and domestication practices. Farmers have engaged in the selection of trees and seeds over generations (Youmbi et al., 2010), choosing seedlings from their own home gardens, and eliminating unproductive trees (in terms of quantity and quality of fruit) but also by sowing seeds with desirable features (Leakey et al., 2009). The modification of selected traits, driven by human intervention, is a key factor in the domestication process of a species such as the African plum (Mboujda et al., 2022). However, the predominantly

allogamous nature of African plum trees and the rare use of vegetative propagation methods, along with environmental conditions, contributes to the maintenance of interindividual variability. Despite an ongoing domestication process, African plums still exhibit a significant phenotypic diversity, in terms of shapes, colors, tastes and sizes supported by observed local nomenclature diversity. This calls for more systematic research on the intraspecific diversity of cultivated perennial species, seen through the lenses of biocultural diversity.

The remarkable finding of our study is the diversity of local names that are rarely shared among respondents, both within each site and along the gradient. Although only five names were shared across all study sites, but many synonyms (African plums that do not have the same name can correspond to very similar fruit features) were observed. For instance, the ethnovarieties '*feumeu*', and '*apouma*' both designate the same good white plum with green flesh in the Eton language. Synonyms were recurrently observed within local nomenclature systems even when species are clonally reproduced (Dansi et al., 2013; Delêtre, 2009; Mekbib, 2007). In the case of African plum, the naming process exhibits a low level of consistency (the degree of representativeness of the names compared to the actual batch of existing varieties), with unstable meanings. Significant simultaneous exchanges of varieties (African plums as well as names) in Central Cameroon (Rimlinger, Avana, et al., 2021; Rimlinger, Duminil, et al., 2021), particularly through the value chain, can lead to confusion in names. Despite cross-varietal synonyms, the observed local names' diversity can also be attributed to the balance between two selection models: blind selection and intentional selection (Boster, 1984). Cameroonian cultivators employ a differentiated management strategy (Aguirre-Dugua et al., 2012), wherein they maintain desired and cultivated varieties while tolerating unwanted trees that grow spontaneously in the crop fields (Carrière, 2002). This blind or unanticipated selection preserves the entire pool of varieties instead of completely eliminating less appreciated ones (Campbell, 1965), since the cost of maintaining a variety is low compared to the cost of abandoning it. Blind selection goes hand in hand with the intentional selection model based on perceptual distinctiveness, which involves selecting of easily distinguishable characteristics in order to enhance discrimination between diverse cultivars (Boster, 1985). In conclusion, the local nomenclature, which mirrors variation of fruit traits, can also reflect an existing artificial selection, indicating an ongoing process of domestication (Fig. 4). The study of local nomenclature, rooted in collective social-ecological memory, is therefore relevant in the context of agrobiodiversity conservation (Rodríguez Valencia et al., 2019).

Conclusion

The interaction between Beti cultivators and their African plum has resulted in the recognition and naming of a large number of varieties. The local nomenclature of the African plum among the Beti community is rich and motivated based on morphological, organoleptic, topographic, and symbolic features. However, the nomenclature of African plum nomenclature primarily relies on the lexicon, with names reflecting the fruit's morphology or taste, directly influenced by consumer dietary preferences and commercial considerations. External factors, such as seed circulation through regional trade, exchanges, and donations between urban and rural dwellers, as well as among villages, contribute to the diversity of local names along the urban–rural gradient.

The African plum's spontaneous propagation through seed planting allows for weak artificial selection. We posit that this non-intensive artificial selection plays a significant role in the proliferation of local names associated with African plum. In conclusion, recognizing cultivators' knowledge and preferences regarding the varieties they maintain in their fields is crucial for understanding the possible loss of germplasm diversity in agricultural systems and implementing effective in situ conservation measures.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10745-023-00427-8>.

Acknowledgements The authors thank the tree owners who generously participated in this study. We warmly thank all the facilitators in the field and the people who generously hosted us. We also acknowledge Inga Beyers (University of Hannover) and Eric Antoine Gonzalez (University of Clemson) for copyediting this paper and three anonymous referees for their helpful comments on an earlier draft of the manuscript.

Author Contributions S.C., J.D. and A.R. planned and designed the research. M.T. and T.L. conducted fieldwork and interviews. T.L. analysed the data. A.R., S.C. and T.L. wrote the first version of the manuscript, with inputs from J.D., C.L. and V.L.. All authors read and approved the final version of the manuscript.

Funding Open access funding provided by University of Lausanne. This project has been supported by Agropolis Fondation under the reference ID 1605-042 through the « Investissements d'avenir » program (Labex Agro: ANR-10-LABX-0001-01), under the frame of I-SITE MUSE (ANR-16-IDEX-0006). Doctoral fieldwork was supported by the Agence Universitaire de la Francophonie, Bureau d'Europe de l'Ouest.

Availability of Data and Materials The data sets supporting the conclusions of this article are available in the following OSF repository: https://osf.io/g56t3/?view_only=41a5e8f5f53b4bbda6cee441f3f350f4.

Declarations

Ethics Approval and Consent to Participate For each study site, local traditional authorities were visited to obtain their agreement to conduct interviews in the area under their authority. Prior to conduct interviews,

participants were informed orally of the research intentions and of their right to participate or decline. A written format indicating that participants agreed that the interview followed the principle of prior informed consent was signed after interview completion.

Competing Interests The authors have no competing interests to declare that are relevant to the content of this article.

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References

- Adan, N., Atchison, J., Reis, M. S., & Peroni, N. (2016). Local knowledge, use and management of ethnovarieties of *Araucaria angustifolia* (Bert.) Ktze. in the Plateau of Santa Catarina, Brazil. *Economic Botany*, 70(4), 353–364. <https://doi.org/10.1007/s12231-016-9361-z>
- Agbo, R. I., Vihotogbé, R., Missihoun, A. A., Dagba, R. A., Assogbadjo, A. E., & Agbangla, C. (2020). Indigenous knowledge of *Detarium microcarpum* Guill. & Perr. (Caesalpinaceae) and implication for conservation in Benin (West Africa). *Environment, Development and Sustainability*, 22(7), 6261–6285. <https://doi.org/10.1007/s10668-019-00477-3>
- Aguirre-Dugua, X., Eguarte, L. E., González-Rodríguez, A., & Casas, A. (2012). Round and large: Morphological and genetic consequences of artificial selection on the gourd tree *Crescentia cujete* by the Maya of the Yucatan Peninsula, Mexico. *Annals of Botany*, 109(7), 1297–1306. <https://doi.org/10.1093/aob/mcs068>
- Ajibesin, K. K. (2011). *Dacryodes edulis* (G. Don) H. J. Lam: A review on its medicinal, phytochemical and economical properties. *Research Journal of Medicinal Plant*, 5(1), 32–41.
- Anegbeh, P. O., Ukafor, V., Usoro, C., Tchoundjeu, Z., Leakey, R. R. B., & Schreckenber, K. (2005). Domestication of *Dacryodes edulis*: 1. Phenotypic variation of fruit traits from 100 trees in southeast Nigeria. *New Forests*, 29(2), 149–160. <https://doi.org/10.1007/s11056-005-0266-4>
- Appa Rao, S., Bounphanousay, C., Schiller, J. M., Alcantara, A. P., & Jackson, M. T. (2002). Naming of traditional rice varieties by farmers in the Lao PDR. *Genetic Resources and Crop Evolution*, 49(1), 83–88. <https://doi.org/10.1023/A:1013843913975>
- Assogbadjo, A. E., Glèlè Kakaï, R., Chadare, F. J., Thomson, L., Kyndt, T., Sinsin, B., & Van Damme, P. (2008). Folk Classification, Perception, and Preferences of Baobab Products in West Africa: Consequences for Species Conservation and Improvement. *Economic Botany*, 62(1), 74–84. <https://doi.org/10.1007/s12231-007-9003-6>
- Aswani, S., Ferse, S. C. A., Stähler, M., & Chong-Montenegro, C. (2020). Detecting change in local ecological knowledge: An application of an index of taxonomic distinctness to an ethnoichthyological classification in the Solomon Islands. *Ecological Indicators*, 119, 106865.

- Awono, A., Ndoye, O., Schreckenber, K., Tabuna, H., Isseri, F., & Temple, L. (2002). Production and Marketing of Safou (*Dacryodes edulis*) in Cameroon and Internationally: Market Development Issues. *Forests, Trees and Livelihoods*, 12(1–2), 125–147. <https://doi.org/10.1080/14728028.2002.9752416>
- Boster, J. S. (1984). Inferring decision making from preferences and behavior: An analysis of Aguaruna Jívaro manioc selection. *Human Ecology*, 12(4), 343–358. <https://doi.org/10.1007/BF01531123>
- Boster, J. S. (1985). Selection for perceptual distinctiveness: Evidence from aguaruna cultivars of *Manihot esculenta*. *Economic Botany*, 39(3), 310–325. <https://doi.org/10.1007/BF02858802>
- Campbell, D. T. (1965). Variation and selective retention in socio-cultural evolution. In *Social change in developing areas: A reinterpretation of evolutionary theory* (eds. Barringer, H.R., Blanksten, G.I. & Mack, R.W.).
- Carrière, S. M. (2002). Orphan trees of the forest: Why do Ntumu farmers of Southern Cameroon protect trees in their swidden fields. *Journal of Ethnobiology*, 22(1), 133–162.
- Chevalier, A. (1949). Quelques arbres fruitiers et oléagineux peu connus de l'Afrique tropicale: Canaris et Safous. *Journal D'agriculture Traditionnelle Et De Botanique Appliquée*, 29(321), 385–395. <https://doi.org/10.3406/jatba.1949.6707>
- Dansi, A., Dantsey-Barry, H., N'Kpenu, E. K., Agré, A. P., Sunu, Y. D., Kombaté, K., Loko, Y. L., Dansi, M., Assogba, P., & Vodouhè, R. (2013). Varietal diversity and genetic erosion of cultivated yams (*Dioscorea cayenensis* Poir—*D. rotundata* Lam complex and *D. alata* L.) in Togo. *International Journal of Biodiversity and Conservation*, 5(4), 223–239.
- Delètre, M. (2009). *The ins and outs of manioc diversity in Gabon, Central Africa: A pluridisciplinary approach to the dynamics of genetic diversity of Manihot esculenta Crantz (Euphorbiaceae)* [Thesis, Trinity College Dublin]. <https://tel.archives-ouvertes.fr/tel-00623219>
- Delètre, M., McKey, D. B., & Hodkinson, T. R. (2011). Marriage exchanges, seed exchanges, and the dynamics of manioc diversity. *Proceedings of the National Academy of Sciences*, 108(45), 18249–18254. <https://doi.org/10.1073/pnas.1106259108>
- Ekué, M. R., Sinsin, B., Eyog-Matig, O., & Finkeldey, R. (2010). Uses, traditional management, perception of variation and preferences in ackee (*Blighia sapida* K. D. Koenig) fruit traits in Benin: Implications for domestication and conservation. *Journal of Ethnobiology and Ethnomedicine*, 6(1), 12. <https://doi.org/10.1186/1746-4269-6-12>
- Gandolfo, E. S., & Hanazaki, N. (2014). Distribution of local plant knowledge in a recently urbanized area (Campeche District, Florianópolis, Brazil). *Urban Ecosystems*, 17(3), 775–785. <https://doi.org/10.1007/s11252-014-0345-4>
- Godoy, R., Reyes-García, V., Byron, E., Leonard, W. R., & Vadez, V. (2005). The effect of market economies on the well-being of indigenous peoples and on their use of renewable natural resources. *Annual Review of Anthropology*, 34(1), 121–138. <https://doi.org/10.1146/annurev.anthro.34.081804.120412>
- Gwali, S., Okullo, J. B. L., Eilu, G., Nakabonge, G., Nyeko, P., & Vuzi, P. (2011). Folk Classification of Shea Butter Tree (*Vitellaria paradoxa* subsp. *Nilotica*) Ethno-varieties in Uganda. *Ethnobotany Research and Applications*, 9(0), Article 0.
- Jagoret, P., Kwesseu, J., Messie, C. A., Michel, I., & Malézieux, É. (2014). Valeurs d'usage des ligneux utilisés en agroforesterie: Les cacaoyères du Centre-Cameroun. *Bois & Forêts des Tropiques*, 321(321), 45. <https://doi.org/10.19182/bft2014.321.a31217>
- Jianchu, X., Yongping, Y., Yingdong, P., Ayad, W. G., & Eyzaguirre, P. B. (2001). Genetic diversity in Taro (*Colocasia esculenta* Schott, Araceae) in China: An ethnobotanical and genetic approach. *Economic Botany*, 55(1), 14–31. <https://doi.org/10.1007/BF02864543>
- Karambiri, M., Elias, M., Vinceti, B., & Grosse, A. (2017). Exploring local knowledge and preferences for shea (*Vitellaria paradoxa*) ethnovarieties in Southwest Burkina Faso through a gender and ethnic lens. *Forests, Trees and Livelihoods*, 26(1), 13–28. <https://doi.org/10.1080/14728028.2016.1236708>
- Kengue, J., Fohouo, F. N. T., & Adewusi, H. G. (2002). Towards the Improvement of Safou (*Dacryodes edulis*): Population Variation and Reproductive Biology. *Forests, Trees and Livelihoods*, 12(1–2), 73–84. <https://doi.org/10.1080/14728028.2002.9752411>
- Labeyrie, V., Caillon, S., Salpeteur, M., & Thomas, M. (2019). Network Analysis: Linking Social and Ecological Dynamics—Methods and Interdisciplinarity—Wiley Online Library. In *Methods and interdisciplinarity* (R. Waldeck, Vol. 1, pp. 69–97). Wiley. <https://doi.org/10.1002/9781119681519.ch4>
- Leakey, R. R. B., Atangana, A. R., Kengni, E., Waruhui, A. N., Usoro, C., Anegbeh, P. O., & Tchoundjeu, Z. (2002). Domestication of *Dacryodes edulis* in West and Central Africa: Characterisation of Genetic Variation. *Forests, Trees and Livelihoods*, 12(1–2), 57–71. <https://doi.org/10.1080/14728028.2002.9752410>
- Leakey, R. R. B., Nevenimo, T., Moxon, J., Pauku, R., Tate, H., & Cornelius, J. (2009). Domestication and improvement of tropical crops for multifunctional farming systems. In *Contemporary crop improvement: A tropical view* (ed. E. Redona, pp. 1–23). QLD.
- Loko, L. E. Y., Toffa, J., Adjatin, A., Akpo, A. J., Orobisi, A., & Dansi, A. (2018). Folk taxonomy and traditional uses of common bean (*Phaseolus vulgaris* L.) landraces by the sociolinguistic groups in the central region of the Republic of Benin. *Journal of Ethnobiology and Ethnomedicine* 14: 52.
- Mainet, H. (2017). Town dwellers in their networks: Urban-rural mobility and household strategies in Cameroon. *Geografisk Tidsskrift-Danish Journal of Geography*, 117(2), 117–129. <https://doi.org/10.1080/00167223.2017.1354715>
- Mala, W. A. (2009). *Knowledge systems and adaptive collaborative management of natural resources in southern Cameroon: Decision analysis of agrobiodiversity for forest-agriculture innovations* [Thesis, Stellenbosch: University of Stellenbosch]. <https://scholar.sun.ac.za:443/handle/10019.1/1290>
- Mboujda, F. M. M., Avana-Tientcheu, M.-L., Momo, S. T., Ntongme, A. M., Vaissayre, V., Azandi, L. N., Dussert, S., Womeni, H., Onana, J.-M., Sonké, B., Tankou, C., & Duminiil, J. (2022). Domestication Syndrome in *Dacryodes edulis* (Burseraceae): Comparison of Morphological and Biochemical Traits between Wild and Cultivated Populations. *Plants*, 11(19), Article 19. <https://doi.org/10.3390/plants11192496>
- Mengue Efangen, C., Temple, L., & Tomekpé, K. (2003). Sélection variétale par des producteurs du Centre du Cameroun. *Infomusa* 12: 4–8.
- Mekbib, F. (2007). Infra-specific folk taxonomy in sorghum (*Sorghum bicolor* (L.) Moench) in Ethiopia: Folk nomenclature, classification, and criteria. *Journal of Ethnobiology and Ethnomedicine*, 3(1), 38. <https://doi.org/10.1186/1746-4269-3-38>
- MINEPAT & PDNP. (2018). *Plan communale de développement (PCD) d'Okola* (p. 278).
- Nuijten, E., & Almekinders, C. J. M. (2008). Mechanisms Explaining Variety Naming by Farmers and Name Consistency of Rice Varieties in The Gambia. *Economic Botany*, 62(2), 148–160. <https://doi.org/10.1007/s12231-008-9012-0>
- Omonhinmin, C. A. (2012). Ethnobotany of *Dacryodes edulis* (G. Don) H. J. Lam in Southern Nigeria I: Practices and applications among the Yoruba speaking people. *Ethnobotany Research and Applications*, 10, 175–184.
- Perales, H. R., Brush, S. B., & Qualset, C. O. (2003). Landraces of maize in Central Mexico: An altitudinal transect. *Economic Botany*, 57(1), 7–20.
- R Development Core Team. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org>








- Reyes-García, V., Martí, N., McDade, T., Tanner, S., & Vadez, V. (2007). Concepts and methods in studies measuring individual ethnobotanical knowledge. *Journal of Ethnobiology*, 27(2), 182–203. [https://doi.org/10.2993/0278-0771\(2007\)27\[182:CAMISM\]2.0.CO;2](https://doi.org/10.2993/0278-0771(2007)27[182:CAMISM]2.0.CO;2)
- Rimlinger, A., Avana, M. L., Awono, A., Chakocho, A., Gakwavu, A., Lemoine, T., Marie, L., Mboujda, F., Vigouroux, Y., Johnson, V., Vinceti, B., Carrière, S. M., & Duminil, J. (2021). Trees and their seed networks: The social dynamics of urban fruit trees and implications for genetic diversity. *PLoS ONE*, 16(3), e0243017. <https://doi.org/10.1371/journal.pone.0243017>
- Rimlinger, A., Carrière, S. M., Avana, M. L., Nguengang, A., & Duminil, J. (2019). The Influence of Farmers' Strategies on Local Practices, Knowledge, and Varietal Diversity of the Safou Tree (*Dacryodes edulis*) in Western Cameroon. *Economic Botany*, 73(2), 249–264. <https://doi.org/10.1007/s12231-019-09455-2>
- Rimlinger, A., Duminil, J., Lemoine, T., Avana, M. L., Chakocho, A., Gakwavu, A., Mboujda, F., Tsogo, M., Elias, M., & Carrière, S. M. (2021). Shifting perceptions, preferences and practices in the African fruit trade: The case of African plum (*Dacryodes edulis*) in different cultural and urbanization contexts in Cameroon. *Journal of Ethnobiology and Ethnomedicine*, 17(1), 65. <https://doi.org/10.1186/s13002-021-00488-3>
- Rivera, D., Obón, C., Heinrich, M., Inocencio, C., Verde, A., & Fajardo, J. (2006). Gathered Mediterranean Food Plants – Ethnobotanical Investigations and Historical Development. *Local Mediterranean Food Plants and Nutraceuticals*, 59, 18–74. <https://doi.org/10.1159/000095207>
- Rodríguez Valencia, M., Davidson-Hunt, I., & Berkes, F. (2019). Social–ecological memory and responses to biodiversity change in a Bribri Community of Costa Rica. *Ambio*, 48(12), 1470–1481. <https://doi.org/10.1007/s13280-019-01176-z>
- Sambatti, J. B. M., Martins, P. S., & Ando, A. (2001). Folk taxonomy and evolutionary dynamics of cassava: A case study in Ubatuba, Brazil. *Economic Botany*, 55(1), 93–105. <https://doi.org/10.1007/BF02864549>
- Sathya, A. (2014). The Art of Naming Traditional Rice Varieties and Landraces by Ancient Tamils. *Asian Agri-History*, 18(1), 5–21.
- Schreckenberg, K., Awono, A., Degrande, A., Mboosso, C., Ndoye, O., & Tchoundjeu, Z. (2006). Domesticating Indigenous Fruit Trees as a Contribution to Poverty Reduction. *Forests, Trees and Livelihoods*, 16(1), 35–51. <https://doi.org/10.1080/14728028.2006.9752544>
- Schreckenberg, K., Degrande, A., Mboosso, C., Baboule, Z. B., Boyd, C., Enyong, L., Kanmegne, J., & Ngong, C. (2002). The Social and Economic Importance of *Dacryodes edulis* (G. Don) H. J. Lam in Southern Cameroon. *Forests, Trees and Livelihoods*, 12(1–2), 15–40. <https://doi.org/10.1080/14728028.2002.9752408>
- Sogbohossou, O. E. D., Achigan-Dako, E. G., Komlan, F. A., & Ahanchede, A. (2014). Diversity and Differential Utilization of *Amaranthus* spp. Along the Urban-Rural Continuum of Southern Benin. *Economic Botany*, 18.
- Stampella, P. C. (2016). Local Variability of Citrus (*Citrus* spp.) in Pluricultural Enclaves in the South of Misiones (Argentina): Diversity, Uses and Perception, and Classification of Variability. *Journal of Ethnobiology*, 36(3), 637–657. <https://doi.org/10.2993/0278-0771-36.3.637>
- Tabuna, H. (2007). *Commerce sous-régional et international des produits forestiers non ligneux alimentaires et des produits agricoles traditionnels en Afrique centrale*. FAO.
- Tabuna, H., & Tanoe, M. (2009). Facteurs explicatifs et développement de la consommation actuelle du safou (*Dacryodes edulis*) au Cameroun. *World Agroforestry, Transforming Lives and Landscapes with Trees*, 63.
- Tee, L. H., Yang, B., Nagendra, K. P., Ramanan, R. N., Sun, J., Chan, E.-S., Tey, B. T., Azlan, A., Ismail, A., Lau, C. Y., & Jiang, Y. (2014). Nutritional compositions and bioactivities of *Dacryodes* species: A review. *Food Chemistry*, 165, 247–255. <https://doi.org/10.1016/j.foodchem.2014.05.084>
- Temple, L., & Moustier. (2004). Les fonctions et contraintes de l'agriculture périurbaine de quelques villes africaines (Yaoundé, Cotonou, Dakar). *Cahiers Agricultures*, 13, 15–22.
- Therneau, T., Atkinson, B., & Ripley, B. (2013). Rpart: Recursive Partitioning. R Package Version 3.6.1. <http://CRAN.R-project.org/package=rpart>
- Thomas, M., Dawson, J. C., Goldringer, I., & Bonneuil, C. (2011). Seed exchanges, a key to analyze crop diversity dynamics in farmer-led on-farm conservation. *Genetic Resources and Crop Evolution*, 58(3), 321–338. <https://doi.org/10.1007/s10722-011-9662-0>
- Todou, G. (2015). *Distribution, adaptation environnementale et diversité génétique de Dacryodes buettneri (Engl.) H. J. Lam et Dacryodes edulis (G. Don) H. J. Lam (Burséracées) en Afrique centrale*. Université de Yaoundé 1.
- Van de Velde, M. (2008). *A grammar of Eton* (Mouton de Gruyter). <https://mark.vandavelde.cnrs.fr/project/grammar-of-eton/>
- Vunda, M. (2021). *La valorisation des ressources forestières en Afrique centrale : état des lieux et perspectives de développement à partir des produits forestiers non ligneux (PFNL) en Angola, au Cameroun, au Congo, au Gabon et en République Démocratique du Congo*. Université Clermont Auvergne.
- Waruhiu, A. N., Kengue, J., Atangana, A. R., Tchoundjeu, Z., & Leakey, R. R. (2004). Domestication of *Dacryodes edulis*. 2. Phenotypic variation of fruit traits in 200 trees from four populations in the humid lowlands of Cameroon. *Journal of Food, Agriculture and Environment*, 2, 340–346.
- Youmbi, E., Mbeuyo, M., Tchinda, N. D., & Amougou, A. (2010). Physico-chemical characterisation and classification of fruits of *Dacryodes edulis* from the major agro-ecological zones of Cameroon. *Fruits*, 65(6), 355–365. <https://doi.org/10.1051/fruits/2010030>
- Zamponi, R. (2009). Focus in Fang and other Bantu A70 languages. Siena: Università degli Studi di Siena, ms. Online: https://www2.hu-berlin.de/predicate_focus_africa/data/Zamponi_-_Focus_in_Fang.pdf

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Article S2.

de Tombeur, F., **Lemoine, T.**, Violle, C., Fréville, H., Thorne, S. J., Hartley, S. E., ... & Fort, F. (2022). Nitrogen availability and plant–plant interactions drive leaf silicon concentration in wheat genotypes. *Functional Ecology*, 36(11), 2833-2844.

Nitrogen availability and plant–plant interactions drive leaf silicon concentration in wheat genotypes

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Funding information

Agence Nationale de la Recherche, Grant/Award Number: ANR-19-E32-0011; H2020 European Research Council, Grant/Award Number: ERC-StG-2014-639706-CONSTRAINTS; H2020 Marie Skłodowska-Curie Actions, Grant/Award Number: 101021641

Handling Editor: Julia Cooke

Abstract

1. Estimating plasticity of leaf silicon (Si) in response to abiotic and biotic factors underpins our comprehension of plant defences and stress resistance in natural and agroecosystems. However, how nitrogen (N) addition and intraspecific plant–plant interactions affect Si concentration remains unclear.
2. We grew 19 durum wheat genotypes (*Triticum turgidum* ssp. *durum*) in pots, either alone or in intra- or intergenotypic cultures of two individuals, and with or without N. Above-ground biomass, plant height and leaf [Si] were quantified at the beginning of the flowering stage.
3. Nitrogen addition decreased leaf [Si] for most genotypes, proportionally to the biomass increase. Si plasticity to plant–plant interactions varied significantly among genotypes, with both increases and decreases in leaf [Si] when mixed with a neighbour, regardless of the mixture type (intra-/intergenotype). Besides, increased leaf [Si] in response to plant–plant interactions was associated with increased plant height.
4. Our results suggest the occurrence of both facilitation and competition for Si uptake from the rhizosphere in wheat mixtures. Future research should identify which leaf and root traits characterise facilitating neighbours for Si acquisition. We also show that Si could be involved in height gain in response to intraspecific competition, possibly for increasing light capture. This important finding opens up new research directions on Si and plant–plant interactions in both natural ecosystems and agroecosystems. More generally, our results stress the need to explore leaf Si plasticity in responses to both abiotic and biotic factors to understand plant stress resistance.

KEYWORDS

agroecology, facilitation, genotype mixture, intraspecific variation, nutrient limitation, phenotypic plasticity, plant competition, plant height

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1 | INTRODUCTION

Silicon (Si), taken up from soil as monosilicic acid and deposited in plant tissues as silica ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$), increases plant resistance to a wide range of biotic and abiotic stresses (e.g. water stress, metal toxicity, pathogens and herbivory) (Cooke & Leishman, 2016; Debona et al., 2017; Hartley & DeGabriel, 2016; Massey & Hartley, 2006) and confers mechanical strength to plants (Epstein, 1994; Raven, 1983). The essentiality of Si for plants remains challenging to assess (Coskun et al., 2019; Epstein, 1994) but increased resistance to herbivores and stress alleviation following Si fertilisation can lead to increased plant primary productivity and crop yields (Liang et al., 2015; Savant et al., 1999; Tubana et al., 2016; Xu et al., 2020). Because graminoid crop species can exhibit very high Si concentrations ([Si]) (e.g. up to 20% of SiO_2 in rice; Klotzbücher et al., 2018), the beneficial role of Si in agriculture is well recognised, and Si is routinely applied to croplands in many countries (e.g. China, Japan, USA, Brazil) (Datnoff et al., 2001; Yan et al., 2018). Thus, it is important to understand the factors affecting plant Si nutrition but, to date, we still have limited knowledge of how soil nutrient availability and interactions between plants affect Si concentration.

Increasing evidence suggests that plant Si concentration depends on soil nutrient status (de Tombeur, Laliberté, et al., 2021; Johnson et al., 2021; Minden et al., 2021; Quigley et al., 2020). In particular, decreases in Si concentration and resulting Si-based defences following nitrogen (N) fertilisation have recently been reported for different grassland/pasture species (Johnson et al., 2021; Minden et al., 2021; Quigley et al., 2020) (but see Moise et al., 2019). This has been attributed to the investment in 'cheap' Si versus relatively 'more expensive' carbon (C) (Raven, 1983) during N stress (Johnson et al., 2021; Minden et al., 2021) and reflects trade-offs between plant growth rate and carbon- or Si-based defences within *Poaceae* family (Massey et al., 2007). However, past studies have generally focused only on a single, non-cultivated genotype (Johnson et al., 2021; Minden et al., 2021). Significant genotypic variation in Si concentration has been reported in rice and wheat (Ma et al., 2007; Merah et al., 1999; Talukdar et al., 2019), so the plasticity (i.e. production of multiple phenotypes from a single genotype depending on environmental conditions; Miner et al., 2005) of leaf [Si] in response to N fertilisation might differ among genotypes, but this has not yet been tested.

So far, the influence of plant–plant interactions on plant Si nutrition has received surprisingly little attention in the literature (but see Garbuzov et al., 2011; Ning et al., 2017, 2021), especially compared with other nutrients (Li et al., 2014). At the interspecific level, Ning et al. (2021) showed that rice accumulates significantly more Si when grown with water spinach (*Ipomoea aquatica* Forsk)—a low Si-accumulating species—compared with a rice monoculture, possibly through the effect of root exudates on soil Si mobilisation (de Tombeur, Cornelis, et al., 2021; Ning et al., 2021). However, when two grasses with high Si-concentration (*Poa annua* and *Lolium perenne*) were investigated, such interspecific facilitation on Si concentration was not observed (Garbuzov et al., 2011). The influence

of plant–plant interactions on Si concentration at the intraspecific level, to our knowledge, has received no attention, either in intragenotypic cultures or intergenotypic mixtures. It is important to consider both intra- and intergenotypic cultures because facilitation for Si uptake in the rhizosphere might prevail over competition when genotypes are functionally different (e.g. they contrast in nutrient-acquisition strategies and/or Si demand). Furthermore, both types of genotypic cultures should be considered because intragenotypic stands are typical of modern agriculture, but there is increasing interest in the role of genetic diversity in increasing the sustainability of agriculture as greater intraspecific diversity may increase productivity and resistance to pests and pathogens (Barot et al., 2017; Hajjar et al., 2008; Litrico & Violle, 2015; Montazeaud et al., 2022).

Finally, leaf Si has been linked to different plant architecture traits that could in turn influence competition for light capture, including decreasing leaf insertion angle and leaf arc/straightness (Ando et al., 2002; de Tombeur, Cooke, et al., 2021; Yamamoto et al., 2012; Zanão Júnior et al., 2010), and increasing plant height (Gong et al., 2003; Ma et al., 1989; Zanão Júnior et al., 2010). As such, we might expect some relationships between the Si concentration of a genotype and the outcomes of plant–plant interactions (i.e. in this case, biomass loss or gain when mixed with a neighbour). It remains challenging to predict potential links between Si and competition outcomes, since greater plant height might increase competition intensity (Falster & Westoby, 2003; Violle et al., 2009), but decreasing leaf insertion angle and arc reduces the light extinction coefficient inside the canopy and may thus decrease competition intensity (Ando et al., 2002). Nevertheless, studies on Si benefits against biotic and abiotic stresses have greatly expanded during the last 10 years (Coskun et al., 2019), and investigating previously overlooked functions of silicification, such as its influence on plant architecture and potential impact on plant–plant interactions, is thus needed.

Here, we studied 19 genotypes of durum wheat (*Triticum turgidum* ssp. *durum*), a major staple crop, which we grew in pots, either alone, in intragenotypic culture or in intergenotypic culture, at two levels of N availability. We quantified plant above-ground biomass, plant height and leaf [Si] to (a) evaluate intraspecific variation in leaf [Si] among the 19 genotypes, (b) estimate plasticity of leaf [Si] in response to N fertilisation and plant–plant interactions and (c) explore potential relations between leaf [Si] and competition outcomes. The variation of leaf [Si] among genotypes, as well as plasticity in leaf [Si] in response to N fertilisation, was tested on genotypes grown alone to avoid a neighbour effect. How plant–plant interactions affect leaf [Si], either in intra- or intergenotypic cultures and with or without N addition, was tested by comparing the leaf [Si] of plants alone with that of plants in interaction. Finally, we tested correlations between genotype leaf [Si] and their response to competition in terms of biomass/height losses/gains to explore potential links between [Si] and competition outcomes. We hypothesised a decrease in leaf [Si] following N fertilisation. We further hypothesised that wheat genotypes would vary in both their Si concentrations, and in their response to N fertilisation and plant–plant interactions.

2 | MATERIALS AND METHODS

2.1 | Experimental design

We selected 19 durum wheat genotypes [*T. turgidum* ssp. *Durum* (Desf.)] from the Evolutionary Pre-breeding pOpulation (EPO), a population of 180 genotypes with high phenotypic and genotypic diversities (David et al., 2014). The 19 genotypes represented a large phenotypic diversity on below- and above-ground traits. The 19 genotypes were grown either alone in *single* (alone in the pot), in *intra-genotypic culture* (two plants of the same genotype in the same pot) or in *inter-genotypic culture* (two plants from different genotypes in the same pot), hereafter *growth modalities*, with two levels of N (treatment N⁺ and N⁻), and in triplicate. We randomly assembled 26 *inter-genotypic* mixtures among the 171 possibilities. The modality *single* thus represents 114 individuals (19 genotypes × 2 N levels × 3 replicates), *intra-genotypic culture* 228 individuals (2 plants × 19 genotypes × 2 N levels × 3 replicates) and *inter-genotypic culture* 312 individuals (26 mixtures of 2 plants × 2 N levels × 3 replicates). In total, 384 pots and 654 wheat individuals were considered.

2.2 | Growth conditions

The experiment was conducted at the CEFE experimental field (Montpellier, France) from January to May 2021, in outdoor conditions. We used a randomised complete block design using three blocks (one replicate in each block). Plants were grown in 4-L plastic pots (18.5 cm diameter; 21.5 cm depth) filled with approximately 4.5 kg of local soil (52% sand, 27% silt and 21% clay; 6.9% CaCO₃; 4.1% organic carbon; 0.21% total N; pH 8.0), and amended with PK fertiliser (0.38 g per pot; P₂O₅ and K₂O). The effect of plant–plant interactions on plant Si uptake might be influenced by soil Si availability (Ning et al., 2021). Here, although not quantified, we expect Si availability to be rather high in this young, high-pH and clay + silt-rich soil (Cornelis & Delvaux, 2016). Indeed, a recent analysis of soil Si availability in French soils shows that this soil type exhibits the highest Si concentrations extracted with CaCl₂ and is unlikely to be Si limited (Caubet et al., 2020). Two seeds per plant were sown in each pot and the largest plant was kept after germination. Pots of the N⁺ treatment received N four times during the experiment, for a total input of 0.94 g N per pot, whereas pots of the N⁻ treatment did not receive any N fertilisation. Plants were not protected from the rain and were watered with amounts to avoid water excess or deficit.

2.3 | Plant height, biomass and leaf [Si] measurements

Vegetative plant height, plant above-ground biomass and leaf [Si] were quantified at the beginning of the flowering stage.

Vegetative height was measured as the distance between the soil surface and the tallest leaf without stretching the plant leaf. The leaf [Si] was quantified with an X-ray fluorescence spectrometer (Reidinger et al., 2012). Briefly, three most recent ligulate adult leaves were sampled on each individual, dried at 60°C for 72 h and ball-milled (Retsch MM400 Mixer mill) for 3 min at a frequency of 20 Hz. Ground samples were pressed at 10 tons into pellets using a manual hydraulic press (Specac). Si analyses were performed using a Nitron XL3t900 GOLDD XRF analyser (Thermo Scientific). Silicon-spiked synthetic cellulose was used for calibration, and analyses were performed under helium atmosphere to avoid signal loss by air absorption (Reidinger et al., 2012). A reading was taken of each side of the pellet, approximately 1 h apart, to account for *u*-drift in the instrument (Johnson, 2014). The concentration of Si in these three most recent ligulate adult leaves (in % of Si by dry weight) was considered to capture the intraspecific variation in leaf [Si] among the genotypes, the response to N fertilisation and plant–plant interactions, and potential relations between leaf [Si] and competition outcomes. Finally, all plant materials were harvested, dried at 60°C for 72 h and weighed to obtain above-ground biomass.

2.4 | Statistical analyses

2.4.1 | Variation in leaf [Si] among genotypes and response to N fertilisation

Variation in leaf [Si] among the 19 wheat genotypes and their plasticity to N fertilisation were assessed only for the *single* plants to discriminate it from the neighbour effect. For both N treatments, differences in leaf Si across the 19 genotypes were tested by a one-way analysis of variance (ANOVA). To quantify the plasticity of leaf [Si] in response to N fertilisation among the 19 genotypes, we calculated log response-ratios (hereafter logRR) as the logarithm of ratios between individual trait values and corresponding genotype-mean values in N⁻, as follows:

$$\log\text{RR} = \log_{10}\left(\frac{\text{leaf}[\text{Si}]_{\text{N}^+}}{\text{leaf}[\text{Si}]_{\text{N}^-}}\right).$$

Differences in logRR among genotypes were tested by ANOVA, and genotype-mean logRR significantly different from zero were assessed with Student's *t*-tests. A logRR below zero means that the treatment significantly decreased the trait values, while the opposite is true for logRR above zero.

2.4.2 | Plasticity to plant–plant interactions

We first tested differences in leaf [Si] among the treatments *single*, *intra*- and *inter-genotypic cultures* by ANOVA followed by post hoc tests using the 'MULTCOMP' package (Hothorn et al., 2008) for both

N treatments. To quantify the plasticity of leaf [Si] to plant–plant interactions, we calculated logRR as the logarithm of ratios between individual trait values and corresponding genotype-mean values in *single*, independently for both N treatments. *Intra-* and *intergenotypic culture* treatments were considered either separately or pooled together as a global factor ‘plant–plant interactions’ to contrast single versus two-plant cultures in the analyses. Spearman rank correlation coefficients were calculated to test whether the ranking in genotype-mean logRR were conserved between both N treatments and between *intra-* and *intergenotypic cultures*. For the *intergenotypic culture* treatment, we further tested if neighbour identity influenced leaf [Si] by ANOVA, and for both N treatments.

2.4.3 | Relationships between leaf [Si], plant height and biomass

We first tested differences in plant above-ground biomass and plant height across the different treatments (N and growth modality) by ANOVA, followed by post hoc tests. Relationships between above-ground biomass/plant height (dependent variables) and leaf [Si] (independent variable) were then tested through mixed-effect models with genotype identity as a random factor, using the package ‘NLME’ (Pinheiro et al., 2022). Models involving only the *single* individuals included both N treatments to test if a N-induced decrease in biomass affects leaf [Si], while models considering only plants with a neighbour were run separately for each N treatment.

To test whether high-Si genotypes lost more or gain more biomass as a response to plant–plant interactions, we tested the significance of relationships between the logRR of plant biomass in response to plant–plant interactions and genotype-mean leaf [Si] in *single* by regression analyses, and for both N treatments.

For each model, residuals were inspected visually to check assumptions. Appropriate variance structures were specified in a second model if required (Zuur et al., 2009). All analyses were conducted in the R environment (R Core Team, 2021).

3 | RESULTS

3.1 | Intraspecific variation in leaf [Si] and plasticity to N fertilisation

Without N fertilisation, genotype-mean leaf [Si] ranged from 1.0% to 2.9%, but did not significantly differ among genotypes ($p = 0.09$, Figure 1a). N fertilisation resulted in an overall decrease in leaf [Si] of 42%, with genotype-mean ranging from 0.7% to 1.9% and that differed significantly among genotypes (Figure 1a). The response of leaf [Si] to N fertilisation (logRR) varied significantly among genotypes, and N fertilisation significantly decreased leaf [Si] for 12 out of the 19 genotypes (logRR < 0) (Figure 2a).

3.2 | Plasticity to plant–plant interactions

We found no overall effect of growth modality (*single*, *intra-* or *intergenotypic culture*) on leaf [Si], whether plants were N-fertilised or not (Figure 1b). However, plasticity in leaf [Si] in response to plant–plant interactions (logRR) varied significantly among genotypes for both N treatments (Figure 2b). The presence of a neighbour significantly decreased leaf [Si] for seven genotypes in the N⁻ and for five genotypes in the N⁺ treatments (logRR < 0), and significantly increased leaf [Si] for three genotypes in the N⁻ and for seven genotypes in the N⁺ treatments (logRR > 0) (Figure 2b).

Genotypes varied significantly in their responses to plant–plant interactions also within the *intra-* and *intergenotypic culture* treatments and for both N treatments (see Figure S1). Genotype-mean responses were not consistent between N treatments (Spearman's coefficient $\rho = -0.06$ and $p = 0.80$ for intragenotypic culture; $\rho = -0.12$ and $p = 0.64$ for intergenotypic culture) but were consistent between the *inter-* and *intra-*genotypic culture treatments ($\rho = 0.75$ and $p < 0.001$ for N⁻; $\rho = 0.73$ and $p < 0.001$ for N⁺). Despite this, in the *intergenotypic culture* treatment, the responses of leaf [Si] to plant–plant interactions significantly varied with neighbour identity in N⁻ (Figure 3). In particular, leaf [Si] responses were significantly below 0 for three neighbours and above 0 for one neighbour. Interestingly, this latter neighbour (GQ4X76) had the highest positive effect of leaf [Si] also in N⁺ (Figure 3).

3.3 | Plant height, above-ground biomass and responses to N fertilisation and plant–plant interactions

Overall, N fertilisation increased plant biomass and height, while the presence of a neighbour decreased biomass for both N treatments but had no significant effect on plant height (Figure 1c,d).

We found a strong significant negative relationship between leaf [Si] and above-ground biomass, but not plant height, for *single* plants (model including both N treatments) (Table 1). We found a strong negative relationship between the plasticity (logRR) in leaf [Si] and that of biomass in response to N fertilisation (Figure 4a), suggesting that larger increase in plant biomass following N fertilisation implied a stronger decrease in leaf [Si], and confirming the strong dependency between these two traits when N was manipulated. In contrast, plasticity of plant height to N fertilisation was not related to that of leaf [Si] (Figure 4a).

In the models considering plants with a neighbour, we also observed a slight negative relationship between leaf [Si] and above-ground biomass, but only in the N⁻ treatment (Table 1). When *intra-* and *intergenotypic culture* were considered separately, none of the biomass-Si relationships were significant (Table S1). However, significant positive relationships between plant height and leaf [Si] were identified for both N treatments (Table 1), and within the *intra-* and *intergenotypic culture* (Table S1).

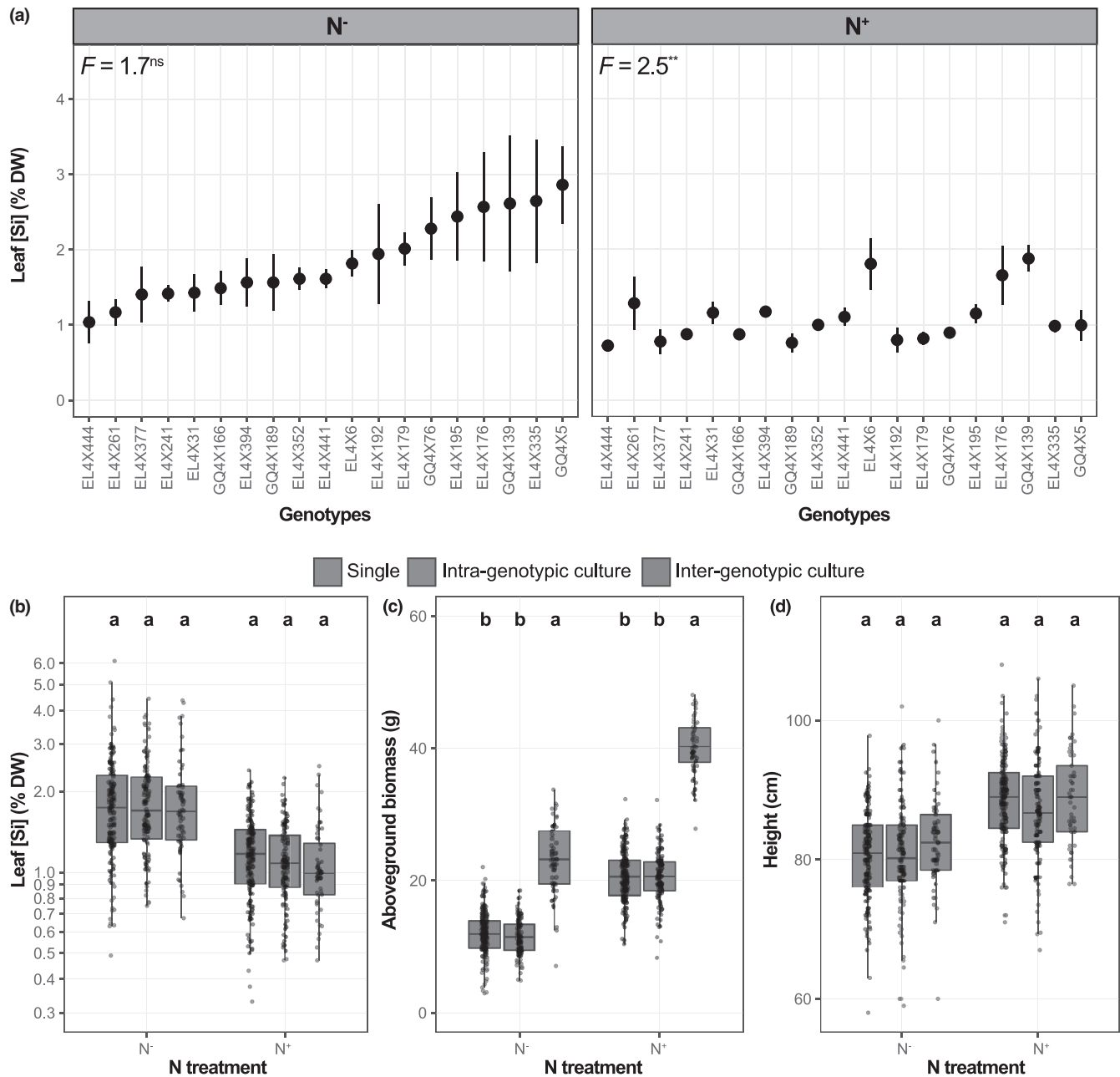


FIGURE 1 Leaf silicon concentrations ([Si]) of 19 durum wheat genotypes grown alone (*single*) and for two levels of N availability (means \pm SE; $n = 3$) in (a). Boxplots showing the effects of plant growth modalities (*single*, *intra-* and *intergenotypic culture*) on leaf [Si] in (b), plant above-ground biomass in (c) and plant height in (d), for each N treatment. In (a), data are ranked by increasing genotype-mean leaf [Si] in the N⁻ treatment for both plots, and results of ANOVA (F -values) conducted between the genotypes are given. In (b)–(d), the central horizontal bar in each box shows the median, the box represents the interquartile range (IQR) and the whiskers show the location of the most extreme data points that are still within a factor of 1.5 of the upper or lower quartiles. Each point indicates one individual, and the y-axis for leaf [Si] in (b) is on a logarithmic scale to improve visualisation. Different letters indicate significant differences ($p < 0.05$) between *single*, *intra-* and *intergenotypic culture* within an N treatment. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns, not significant.

Plasticity in plant biomass and plasticity in height to the presence of a neighbour were significantly related to genotype-mean leaf [Si] in the N⁻ treatment but only very slightly (Figure S2), suggesting a limited control of genotype leaf [Si] on competition outcomes. However, plasticity in plant height and plasticity in leaf [Si] to the presence of a neighbour were positively related for

both N treatments (Figure 4b) and within *intra-* and *intergenotypic culture* (Figure S3), suggesting that increased leaf [Si] for plants in interaction implied an increase in plant height. In contrast, plasticity of above-ground biomass to plant–plant interactions was not related to that of leaf [Si], except slightly in N⁻ (Figure 4b; Figure S3).

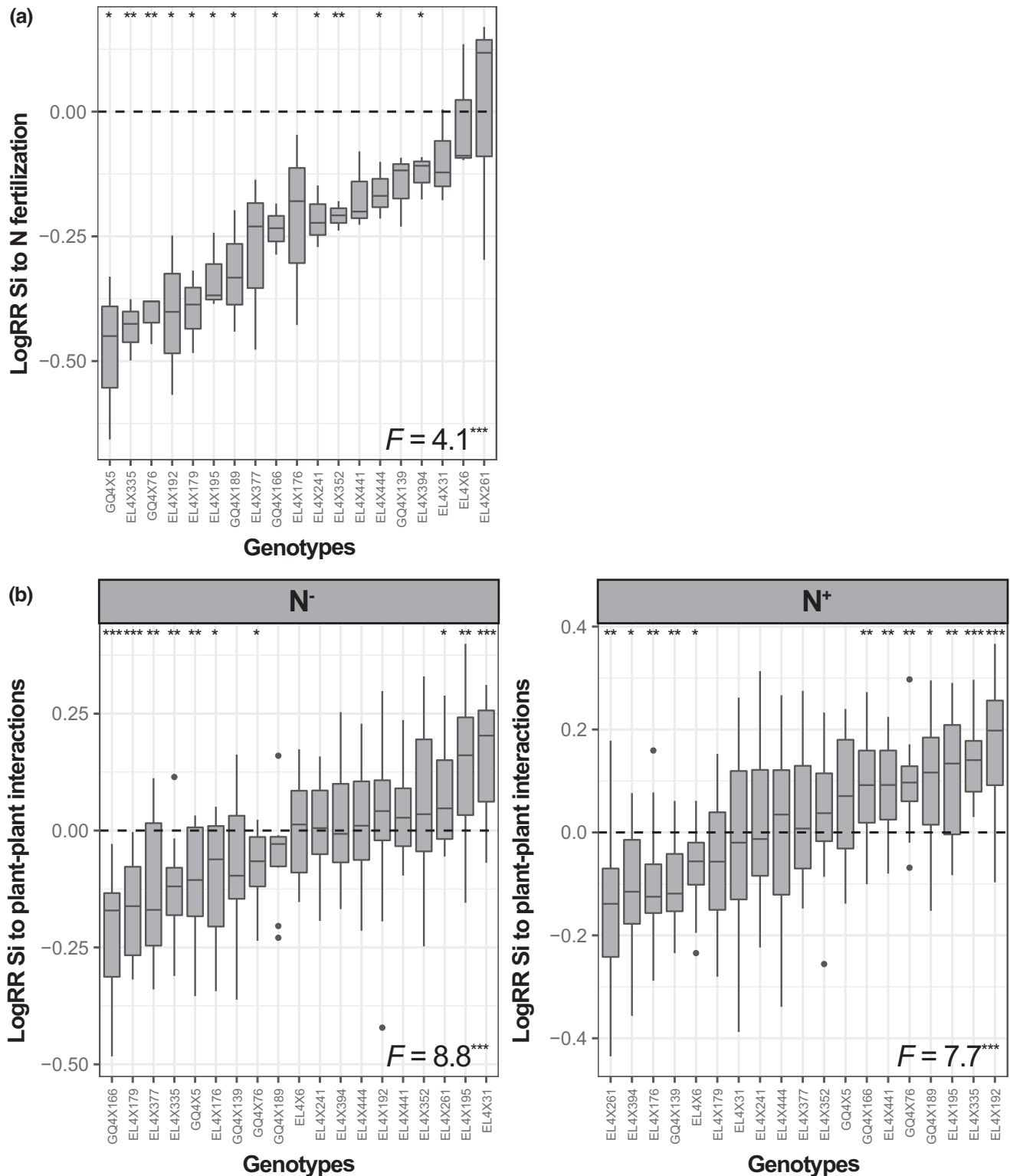


FIGURE 2 Variation in log response ratios (logRR) of leaf silicon (Si) concentrations to nitrogen (N) fertilisation for the *single plants* in (a) and to plant–plant interactions for both N treatments in (b) among 19 wheat genotypes. Both *intra-* and *intergenotypic culture* were considered together in the analysis in (b) (see Figure S1 for separate analyses). Data are ranked by increasing genotype-mean logRR. The central horizontal bar in each box shows the median, the box represents the interquartile range (IQR), the whiskers show the location of the most extreme data points that are still within a factor of 1.5 of the upper or lower quartiles, and black points are values that fall outside the whiskers. Results of ANOVA (F -values) conducted between the genotypes are given. LogRR significantly different from zero following student t -tests are indicated with stars. $***p < 0.001$; $**p < 0.01$; $*p < 0.05$; ns, not significant.

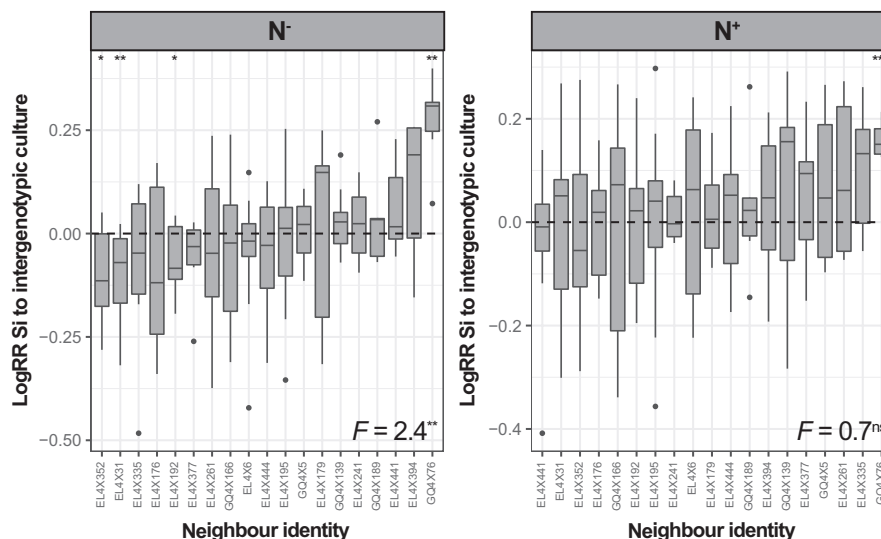


FIGURE 3 Variation in log response ratios (logRR) of leaf silicon (Si) concentrations to *intergenotypic culture* for both N treatments as a function of neighbour identity. Data are ranked by increasing neighbour identity-mean logRR for both plots. The central horizontal bar in each box shows the median, the box represents the interquartile range (IQR), the whiskers show the location of the most extreme data points that are still within a factor of 1.5 of the upper or lower quartiles, and black points are values that fall outside the whiskers. Results of ANOVA (F -values) conducted between the neighbour identity are given. LogRR significantly different from zero following student t -tests are indicated with stars for the N^- treatment. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns, not significant.

TABLE 1 Results of the mixed-effect models (genotype as random factor) testing the effects of leaf silicon (Si) concentrations on above-ground plant biomass and height for *single* plants (both nitrogen (N) levels in the analyses), and for plants in interactions for both N levels separately (*intra-* and *intergenotypic* treatments combined; see Table S1 for separated analyses)

	Single			Inter- and intragenotypic culture					
	N ⁻ and N ⁺ combined			N ⁻			N ⁺		
	Slope	F -value	p -value	Slope	F -value	p -value	Slope	F -value	p -value
Biomass ~ Leaf Si	-8.4	74.6	<0.001	-0.6	4.8	<0.05	-0.5	0.6	0.43
Height ~ Leaf Si	-1.6	4.2	<0.05	1.8	11.1	<0.001	5.6	31.7	<0.001

4 | DISCUSSION

We demonstrate that durum wheat genotypes markedly differ in both their Si concentrations and response to N fertilisation and plant-plant interactions. Despite contrasting responses among genotypes, N fertilisation predominantly decreased leaf Si concentrations. The responses to plant-plant interactions were less clear, with both increases and decreases in leaf [Si] in the presence of a neighbour among the studied wheat genotypes. The genotypic responses to plant-plant interactions were rather consistent between *intra-* and *intergenotypic cultures*, even though neighbour identity seemed to play a slight role in Si concentrations, at least in N^- . We also show that the leaf [Si] of a given genotype has a limited influence on its biomass gain/loss when mixed with a neighbour. However, we show that increased leaf [Si] in response to competition was associated with increased plant height, which could have a role in light capture.

The strong decrease in Si concentrations following N fertilisation confirms our hypothesis and previous studies using natural

grassland/pasture species (Johnson et al., 2021; Massey et al., 2007; Minden et al., 2021; Quigley et al., 2020). The results are also in line with the resource availability hypothesis, which proposes higher levels of defence in resource-limited environments (Coley et al., 1985; Endara & Coley, 2011). Since Si is thought to incur lower C costs than C-based structural/defensive compounds (Raven, 1983), this might also reflect a selective advantage of plants reducing leaf construction/defence costs when resources are limiting (Minden et al., 2021), but the underlying mechanism remains unclear (Hodson & Guppy, 2022). Although N deficiency might directly increase the expression of Si transporters (Wu et al., 2017), our results suggest a N-driven 'dilution effect' on leaf [Si] (Hodson & Guppy, 2022; Jarrell & Beverly, 1981) since we found a strong negative relation between biomass and leaf [Si]. This likely explains the strong negative relationship between the plasticity of biomass and that of leaf [Si] to N fertilisation. The significant interactions between wheat Si concentrations, total above-ground biomass and responses to N fertilisation stress the need to combine data on total Si content and total dry matter content, wherever possible (Jarrell & Beverly, 1981).

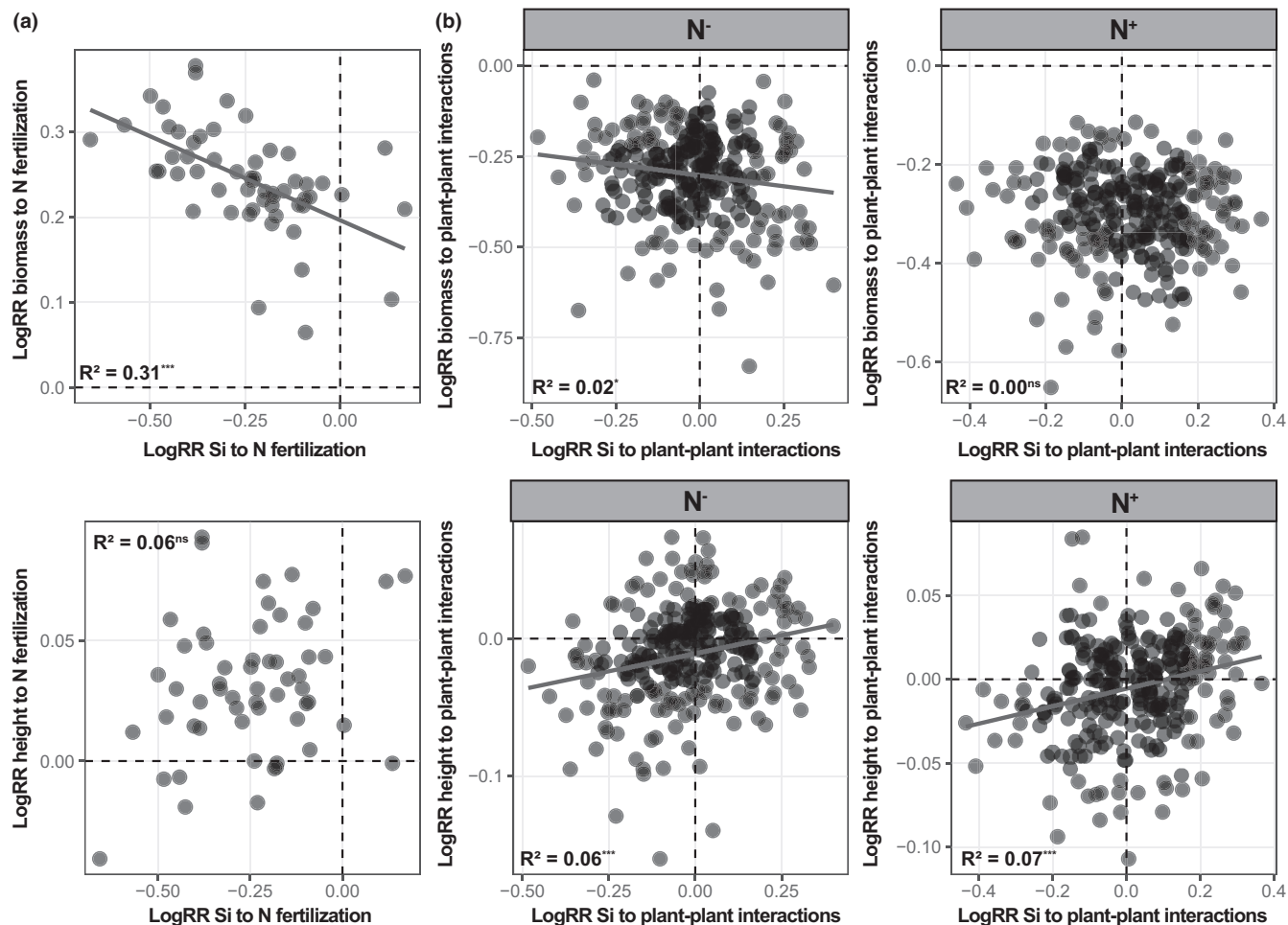


FIGURE 4 Relationships between the log response ratio (logRR) of leaf silicon (Si) concentrations and those of biomass and height to nitrogen (N) fertilisation for the *single* in (a) and to plant–plant interactions for both N treatments in (b). Both *intra*- and *intergenotypic* culture were considered together as ‘plant–plant interactions’ in the analyses (see Figure S3 for separate analyses). Red lines indicate regression lines between variables, and multiple R -squared are given. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns, not significant.

Despite the significantly lower biomass of plants in mixtures compared with that of plants grown alone in pots, growth modality did not significantly influence leaf [Si] overall. However, the response of leaf [Si] to a neighbour presence strongly varied among the 19 wheat genotypes, and neighbour identity influenced the responses of leaf [Si] to plant–plant interactions in N^- , in the *intergenotypic* culture treatment. So far, facilitation for Si uptake in the rhizosphere has been demonstrated at the interspecific level with functionally contrasting species (e.g. contrast in Si demand and/or nutrient-acquisition strategies; Ning et al., 2021). Our results suggest that both competition and facilitation for Si uptake might exist at the intraspecific level with durum wheat genotypes. Our comprehension of root-related processes influencing Si mobilisation in the rhizosphere is still limited, despite some progress in recent years (de Tombeur, Cornelis, et al., 2021; Frew et al., 2017; Gattullo et al., 2016). Grasses release siderophores (i.e. low-molecular weight chelators) in the soil solution to acquire limited nutrients (Ma, 2005; Oburger et al., 2014; Römheld, 1991), which also increase Si availability (Gattullo et al., 2016). This mechanism

could possibly explain the increases of leaf [Si] of some mixtures (either *intra*- and *intergenotypic* mixtures), and why some genotypes (especially GQ4X76) consistently induced an increase of leaf [Si] of their neighbours.

A potential impact of genotype leaf [Si] on competition outcomes might be expected, since Si is involved in traits linked with plant architecture and light capture (Ando et al., 2002; de Tombeur, Cooke, et al., 2021; Yamamoto et al., 2012; Zañão Júnior et al., 2010). However, despite a slightly positive relationship between genotype-mean leaf [Si] in *single* and the response of above-ground biomass to competition in the N^- treatment, genotype leaf [Si] did not appear to play a major role in *intra*- or *intergenotypic* competition outcomes. Nevertheless, increased leaf [Si] in response to competition was associated with increased plant height, and this was the case for both N and mixture treatments. Si might play an indirect role in intraspecific competition through its influence on plant height, given that this trait is often associated with a strong competitive ability in wheat (Thomas et al., 1993; Yenish & Young, 2004) and more generally with light capture (Falster &

Westoby, 2003; Violle et al., 2009). Height gain following Si fertilisation is, however, also associated with straighter leaves with lower leaf insertion angle (Zanão Júnior et al., 2010), which might in turn reduce the light extinction coefficient inside the canopy (Ando et al., 2002). In any case, this finding opens up new research directions on Si and plant–plant interactions in both natural and agroecosystems which remain strikingly scarce to date (but see Garbuzov et al., 2011; Ning et al., 2017, 2021).

Several perspectives arise from the results discussed above. First, the observed intragenotypic variation in leaf [Si] might be linked to the expression of Si transporters (Ma et al., 2007), which should be tested among the 180 EPO durum wheat genotypes. Finding a consistent pattern among genotype leaf [Si] and the expression of Si transporters at the intraspecific level would improve our understanding of the evolutionary path of Si uptake by vascular plants (Deshmukh et al., 2020; Deshmukh & Bélanger, 2016). Second, since genotype leaf [Si] directly influences levels of silica-based defences (Hartley et al., 2015; McLarnon et al., 2017) and their responses to abiotic stresses (Thorne et al., 2022), breeding for Si-rich crop genotypes may have benefits for reducing pesticide inputs, especially in low-nutrient and/or herbivore susceptible areas (Christian et al., 2022). Regarding N fertilisation, genotypes for which leaf [Si] did not decrease might be retained by plant breeders to limit the N-driven decrease in silica-based defences. Regarding plant–plant interactions, genotypes for which leaf [Si] increased when mixed with a neighbour might be preferred for their potentially greater ability to accumulate Si and cope with environmental stresses, either in intra- or intergenotypic cultures. Third, the strong N-driven decrease in plant Si concentrations—and most likely resulting silica-based defences—may have detrimental effects on herbivore attacks (Johnson et al., 2021) and resulting crop sustainability and food security (Sundström et al., 2014). Such negative feedback could be mitigated through the use of Si fertilisers, even though it comes with potential drawbacks and significant C footprints (Thorne et al., 2020). Implementing agricultural practices that have positive impacts on soil–plant Si mobility (e.g. cereal-legume intercropping, cover crops; no-till farming; de Tombeur, Roux, et al., 2021; Li et al., 2020) might mitigate this negative feedback. Finally, our results suggest the existence of ‘good neighbours’ that facilitate Si uptake. Future research should identify which root chemical and physical traits characterise these facilitators, for the future development of productive and stress-resistant genotypes mixtures, that is, ideomixes (Litrice & Violle, 2015). Furthermore, facilitation/competition for plant Si uptake should be tested for different soil types with contrasting Si availability because the effect of plant–plant interactions on plant Si uptake is influenced by soil Si availability (Ning et al., 2021).

AUTHOR CONTRIBUTIONS

Cyrille Violle, Florian Fort and Taïna Lemoine conceived the ideas; Cyrille Violle, Florian Fort, Hélène Fréville and Taïna Lemoine designed the experiment; Taïna Lemoine and Sarah J. Thorne collected the data; Felix de Tombeur analysed the data and led the writing of

the manuscript. All authors contributed critically to drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We are grateful to Elodie Certenais, Leo Streith, Maëva Tremblay and Robin Latapie for their invaluable help both in the field and in the lab. We also thank the TE platform team of the LabEx CeMEB for all the help provided to conduct the experiment. This project has received funding from the European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement no. 101021641 (project SiliConomic granted to F.d.T.), from the European Research Council (ERC) Starting grant ‘Ecophysiological and biophysical constraints on domestication in crop plants’ (grant no. ERC-StG-2014-639706-CONSTRAINTS) awarded to C.V., and by the Agence Nationale de la Recherche (ANR) project ‘Selecting for cooperative crops to develop sustainable agriculture’ (SCOOP, grant no. ANR-19-E32-0011) awarded to H.F. Open access publishing facilitated by The University of Western Australia, as part of the Wiley - The University of Western Australia agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST

C.V. is an Associate Editor of Functional Ecology but took no part in the peer review and decision-making processes for this paper. The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.x3ffbg7nj> (de Tombeur et al., 2022).

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REFERENCES

- Ando, H., Kakuda, K. I., Fujii, H., Suzuki, K., & Ajiki, T. (2002). Growth and canopy structure of rice plants grown under field conditions as affected by Si application. *Soil Science and Plant Nutrition*, 48(3), 429–432. <https://doi.org/10.1080/00380768.2002.10409221>
- Barot, S., Allard, V., Cantarel, A., Enjalbert, J., Gauffreteau, A., Goldringer, I., Lata, J. C., Le Roux, X., Niboyet, A., & Porcher, E. (2017). Designing mixtures of varieties for multifunctional agriculture with the help of ecology. A review. *Agronomy for Sustainable Development*, 37(2), 1–20. <https://doi.org/10.1007/s13593-017-0418-x>
- Caubet, M., Cornu, S., Saby, N. P. A., & Meunier, J. D. (2020). Agriculture increases the bioavailability of silicon, a beneficial element for crop, in temperate soils. *Scientific Reports*, 10, 19999. <https://doi.org/10.1038/s41598-020-77059-1>
- Christian, M. M., Shimelis, H., Laing, M. D., Tsilo, T. J., & Mathew, I. (2022). Breeding for silicon-use efficiency, protein content and

- drought tolerance in bread wheat (*Triticum aestivum* L.): A review. *Acta Agriculturae Scandinavica, Section B—Soil & Plant Science*, 72(1), 17–29. <https://doi.org/10.1080/09064710.2021.1984564>
- Coley, P. D., Bryant, J. P., & Chapin, F. S. (1985). Resource availability and plant antiherbivore defense. *Science*, 230, 895–899. <https://doi.org/10.1007/978-94-010-9117-6>
- Cooke, J., & Leishman, M. R. (2016). Consistent alleviation of abiotic stress with silicon addition: A meta-analysis. *Functional Ecology*, 30(8), 1340–1357. <https://doi.org/10.1111/1365-2435.12713>
- Cornelis, J.-T. T., & Delvaux, B. (2016). Soil processes drive the biological silicon feedback loop. *Functional Ecology*, 30(8), 1298–1310. <https://doi.org/10.1111/1365-2435.12704>
- Coskun, D., Deshmukh, R., Sonah, H., Menzies, J. G., Reynolds, O., Ma, J. F., Kronzucker, H. J., & Bélanger, R. R. (2019). The controversies of silicon's role in plant biology. *New Phytologist*, 221(1), 67–85. <https://doi.org/10.1111/nph.15343>
- Datnoff, L. E., Snyder, G. H., & Korndörfer, G. H. (2001). *Silicon in agriculture* (Vol. 8). Elsevier Science.
- David, J., Holtz, Y., Ranwez, V., Santoni, S., Sarah, G., Ardisson, M., Poux, G., Choulet, F., Genthon, C., Roumet, P., & Tavaud-Pirra, M. (2014). Genotyping by sequencing transcriptomes in an evolutionary pre-breeding durum wheat population. *Molecular Breeding*, 34(4), 1531–1548. <https://doi.org/10.1007/s11032-014-0179-z>
- de Tombeur, F., Lemoine, T., Violle, C., Fréville, H., Thorne, S. J., Hartley, S. E., Lambers, H., & Fort, F. (2022). Data from: Nitrogen availability and plant-plant interactions drive leaf silicon concentration in wheat genotypes. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.x3ffbg7nj>
- de Tombeur, F., Roux, P., & Cornelis, J.-T. (2021). Silicon dynamics through the lens of soil-plant-animal interactions: Perspectives for agricultural practices. *Plant and Soil*, 467(1–2), 1–28. <https://doi.org/10.1007/s11104-021-05076-8>
- de Tombeur, F., Cooke, J., Collard, L., Cisse, D., Saba, F., Lefebvre, D., Burgeon, V., Nacro, H. B., & Cornelis, J.-T. (2021). Biochar affects silicification patterns and physical traits of rice leaves cultivated in a desilicated soil (ferric Lixisol). *Plant and Soil*, 460(1–2), 375–390. <https://doi.org/10.1007/s11104-020-04816-6>
- de Tombeur, F., Cornelis, J.-T., & Lambers, H. (2021). Silicon mobilisation by root-released carboxylates. *Trends in Plant Science*, 26(11), 1116–1125. <https://doi.org/10.1016/j.tplants.2021.07.003>
- de Tombeur, F., Laliberté, E., Lambers, H., Faucon, M. P., Zemunik, G., Turner, B. L., Cornelis, J. T., & Mahy, G. (2021). A shift from phenol to silica-based leaf defences during long-term soil and ecosystem development. *Ecology Letters*, 24(5), 984–995. <https://doi.org/10.1111/ele.13713>
- Debona, D., Rodrigues, F. A., & Datnoff, L. E. (2017). Silicon's role in abiotic and biotic plant stresses. *Annual Review of Phytopathology*, 55(1), 85–107. <https://doi.org/10.1146/annurev-phyto-080516-035312>
- Deshmukh, R., & Bélanger, R. R. (2016). Molecular evolution of aquaporins and silicon influx in plants. *Functional Ecology*, 30(8), 1277–1285. <https://doi.org/10.1111/1365-2435.12570>
- Deshmukh, R., Sonah, H., & Belanger, R. (2020). New evidence defining the evolutionary path of aquaporins regulating silicon uptake in land plants. *Journal of Experimental Botany*, 71(21), 6775–6788. <https://doi.org/10.1093/jxb/eraa342>
- Endara, M. J., & Coley, P. D. (2011). The resource availability hypothesis revisited: A meta-analysis. *Functional Ecology*, 25(2), 389–398. <https://doi.org/10.1111/j.1365-2435.2010.01803.x>
- Epstein, E. (1994). The anomaly of silicon in plant biology. *Proceedings of the National Academy of Sciences of the United States of America*, 91(1), 11–17. <https://doi.org/10.1073/pnas.91.1.11>
- Falster, D. S., & Westoby, M. (2003). Plant height and evolutionary games. *Trends in Ecology & Evolution*, 18(7), 337–343. [https://doi.org/10.1016/S0169-5347\(03\)00061-2](https://doi.org/10.1016/S0169-5347(03)00061-2)
- Frew, A., Powell, J. R., Allsopp, P. G., Sallam, N., & Johnson, S. N. (2017). Arbuscular mycorrhizal fungi promote silicon accumulation in plant roots, reducing the impacts of root herbivory. *Plant and Soil*, 419(1–2), 423–433. <https://doi.org/10.1007/s11104-017-3357-z>
- Garbuzov, M., Reidinger, S., & Hartley, S. E. (2011). Interactive effects of plant-available soil silicon and herbivory on competition between two grass species. *Annals of Botany*, 108, 1355–1363. <https://doi.org/10.1093/aob/mcr230>
- Gattullo, C. E., Allegretta, I., Medici, L., Fijan, R., Pii, Y., Cesco, S., Mimmo, T., & Terzano, R. (2016). Silicon dynamics in the rhizosphere: Connections with iron mobilisation. *Journal of Plant Nutrition and Soil Science*, 179(3), 409–417. <https://doi.org/10.1002/jpln.20150535>
- Gong, H. J., Chen, K. M., Chen, G. C., Wang, S. M., & Zhang, C. L. (2003). Effects of silicon on growth of wheat under drought. *Journal of Plant Nutrition*, 26(5), 1055–1063. <https://doi.org/10.1081/PLN-120020075>
- Hajjar, R., Jarvis, D. I., & Gemmill-Herren, B. (2008). The utility of crop genetic diversity in maintaining ecosystem services. *Agriculture, Ecosystems and Environment*, 123(4), 261–270. <https://doi.org/10.1016/j.agee.2007.08.003>
- Hartley, S. E., Fitt, R. N., McLarnon, E. L., & Wade, R. N. (2015). Defending the leaf surface: Intra- and inter-specific differences in silicon deposition in grasses in response to damage and silicon supply. *Frontiers in Plant Science*, 6(February), 35. <https://doi.org/10.3389/fpls.2015.00035>
- Hartley, S. E., & DeGabriel, J. L. (2016). The ecology of herbivore-induced silicon defences in grasses. *Functional Ecology*, 30(8), 1311–1322. <https://doi.org/10.1111/1365-2435.12706>
- Hodson, M. J., & Guppy, C. N. (2022). Some thoughts on silicon and carbon trade-offs in plants. *Plant and Soil*, in press. <https://doi.org/10.1007/s11104-022-05394-5>
- Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50(3), 346–363. <https://doi.org/10.1002/bimj.200810425>
- Jarrell, W. M., & Beverly, R. B. (1981). The dilution effect in plant nutrition studies. *Advances in Agronomy*, 34, 197–224. [https://doi.org/10.1016/S0065-2113\(08\)60887-1](https://doi.org/10.1016/S0065-2113(08)60887-1)
- Johnson, J. (2014). Accurate measurements of low Z elements in sediments and archaeological ceramics using portable X-ray fluorescence (PXRF). *Journal of Archaeological Method and Theory*, 21(3), 563–588. <https://doi.org/10.1007/s10816-012-9162-3>
- Johnson, S. N., Waterman, J. M., Wuhrer, R., Rowe, R. C., Hall, C. R., & Cibils-Stewart, X. (2021). Siliceous and non-nutritious: Nitrogen limitation increases anti-herbivore silicon defences in a model grass. *Journal of Ecology*, 109(11), 3767–3778. <https://doi.org/10.1111/1365-2745.13755>
- Klotzbücher, T., Klotzbücher, A., Kaiser, K., Vetterlein, D., Jahn, R., & Mikutta, R. (2018). Variable silicon accumulation in plants affects terrestrial carbon cycling by controlling lignin synthesis. *Global Change Biology*, 24(1), e183–e189. <https://doi.org/10.1111/gcb.13845>
- Li, L., Tilman, D., Lambers, H., & Zhang, F. S. (2014). Plant diversity and overyielding: Insights from belowground facilitation of intercropping in agriculture. *New Phytologist*, 203(1), 63–69. <https://doi.org/10.1111/nph.12778>
- Li, Z., de Tombeur, F., Vander Linden, C., Cornelis, J. T., & Delvaux, B. (2020). Soil microaggregates store phytoliths in a sandy loam. *Geoderma*, 360(October 2019), 114037. <https://doi.org/10.1016/j.geoderma.2019.114037>
- Liang, Y., Nikolic, M., Bélanger, R., Gong, H., & Song, A. (2015). *Silicon in agriculture—From theory to practice*. Springer Netherlands. <https://doi.org/10.1007/978-94-017-9978-2>
- Litrico, I., & Violle, C. (2015). Diversity in plant breeding: A new conceptual framework. *Trends in Plant Science*, 20(10), 604–613. <https://doi.org/10.1016/j.tplants.2015.07.007>
- Ma, J., Nishimura, K., & Takahashi, E. (1989). Effect of silicon on the growth of rice plant at different growth stages. *Soil Science and*

- Plant Nutrition*, 35(3), 347–356. <https://doi.org/10.1080/00380768.1989.10434768>
- Ma, J. F. (2005). Plant root responses to three abundant soil minerals: Silicon, aluminum and iron. *Critical Reviews in Plant Sciences*, 24(4), 267–281. <https://doi.org/10.1080/07352680500196017>
- Ma, J. F., Yamaji, N., Tamai, K., & Mitani, N. (2007). Genotypic difference in silicon uptake and expression of silicon transporter genes in rice. *Plant Physiology*, 145(3), 919–924. <https://doi.org/10.1104/pp.107.107599>
- Massey, F. P., Ennos, A. R., & Hartley, S. E. (2007). Grasses and the resource availability hypothesis: The importance of silica-based defences. *Journal of Ecology*, 95(3), 414–424. <https://doi.org/10.1111/j.1365-2745.2007.01223.x>
- Massey, F. P., & Hartley, S. E. (2006). Experimental demonstration of the antiherbivore effects of silica in grasses: Impacts on foliage digestibility and vole growth rates. *Proceedings of the Royal Society B: Biological Sciences*, 273(1599), 2299–2304. <https://doi.org/10.1098/rspb.2006.3586>
- McLarnon, E., McQueen-Mason, S., Lenk, I., & Hartley, S. E. (2017). Evidence for active uptake and deposition of Si-based defenses in tall fescue. *Frontiers in Plant Science*, 8(July), 1199. <https://doi.org/10.3389/fpls.2017.01199>
- Merah, O., Deléens, E., & Monneveux, P. (1999). Grain yield, carbon isotope discrimination, mineral and silicon content in durum wheat under different precipitation regimes. *Physiologia Plantarum*, 107(4), 387–394. <https://doi.org/10.1034/j.1399-3054.1999.100403.x>
- Minden, V., Schaller, J., & Olde Venterink, H. (2021). Plants increase silicon content as a response to nitrogen or phosphorus limitation: A case study with *Holcus lanatus*. *Plant and Soil*, 462(1–2), 95–108. <https://doi.org/10.1007/s11104-020-04667-1>
- Miner, B. G., Sultan, S. E., Morgan, S. G., Padilla, D. K., & Relyea, R. A. (2005). Ecological consequences of phenotypic plasticity. *Trends in Ecology & Evolution*, 20(12), 685–692. <https://doi.org/10.1016/j.tree.2005.08.002>
- Moise, E. R. D., McNeil, J. N., Hartley, S. E., & Henry, H. A. L. (2019). Plant silicon effects on insect feeding dynamics are influenced by plant nitrogen availability. *Entomologia Experimentalis et Applicata*, 167(2), 91–97. <https://doi.org/10.1111/eea.12750>
- Montazeaud, G., Flutre, T., Ballini, E., Morel, J.-B., David, J., Girardolle, J., Rocher, A., Ducasse, A., Violle, C., Fort, F., & Fréville, H. (2022). From cultivar mixtures to allelic mixtures: Opposite effects of allelic richness between genotypes and genotype richness in wheat. *New Phytologist*, 233, 2573–2584. <https://doi.org/10.1111/nph.17915>
- Ning, C., Qu, J., He, L., Yang, R., Chen, Q., Luo, S., & Cai, K. (2017). Improvement of yield, pest control and Si nutrition of rice by rice-water spinach intercropping. *Field Crops Research*, 208(April), 34–43. <https://doi.org/10.1016/j.fcr.2017.04.005>
- Ning, C., Wang, L., Liu, R., Pan, T., Cai, Y., Tian, J., Luo, S., & Cai, K. (2021). Plant-mediated rhizospheric interactions in rice and water spinach intercropping enhance Si uptake by rice. *Plant and Soil*, in press. <https://doi.org/10.1007/s11104-021-05199-y>
- Oburger, E., Gruber, B., Schindlegger, Y., Schenkeveld, W. D. C., Hann, S., Kraemer, S. M., Wenzel, W. W., & Puschenreiter, M. (2014). Root exudation of phytosiderophores from soil-grown wheat. *New Phytologist*, 203(4), 1161–1174. <https://doi.org/10.1111/nph.12868>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & Team, R. C. (2022). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-155.
- Quigley, K. M., Griffith, D. M., Donati, G. L., & Anderson, T. M. (2020). Soil nutrients and precipitation are major drivers of global patterns of grass leaf silicification. *Ecology*, 101(6), e03006. <https://doi.org/10.1002/ecy.3006>
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.r-project.org/>
- Raven, J. A. (1983). The transport and function of silicon in plants. *Biological Reviews*, 58, 179–207.
- Reidinger, S., Ramsey, M. H., & Hartley, S. E. (2012). Rapid and accurate analyses of silicon and phosphorus in plants using a portable X-ray fluorescence spectrometer. *New Phytologist*, 195(3), 699–706. <https://doi.org/10.1111/j.1469-8137.2012.04179.x>
- Römheld, V. (1991). The role of phytosiderophores in acquisition of iron and other micronutrients in graminaceous species: An ecological approach. *Plant and Soil*, 130(1–2), 127–134. <https://doi.org/10.1007/BF00011867>
- Savant, N. K., Korndörfer, G. H., Datnoff, L. E., Snyder, G. H., Korndorfer, G. H., Datnoff, L. E., & Snyder, G. H. (1999). Silicon nutrition and sugarcane production: A review. *Journal of Plant Nutrition*, 22(12), 1853–1903. <https://doi.org/10.1080/01904169909365761>
- Sundström, J. F., Albihn, A., Boqvist, S., Ljungvall, K., Marstorp, H., Martiin, C., Nyberg, K., Vagsholm, I., Yuen, J., & Magnusson, U. (2014). Future threats to agricultural food production posed by environmental degradation, climate change, and animal and plant diseases—A risk analysis in three economic and climate settings. *Food Security*, 6(2), 201–215. <https://doi.org/10.1007/s12571-014-0331-y>
- Talukdar, P., Hartley, S. E., Travis, A. J., Price, A. H., & Norton, G. J. (2019). Genotypic differences in shoot silicon concentration and the impact on grain arsenic concentration in rice. *Journal of Plant Nutrition and Soil Science*, 182(2), 265–276. <https://doi.org/10.1002/jpln.20180373>
- Thomas, J. B., Schaalje, G. B., & Grant, M. N. (1993). Height, competition and yield potential in winter wheat. *Euphytica*, 74(1–2), 9–17. <https://doi.org/10.1007/BF00033761>
- Thorne, S. J., Hartley, S. E., & Maathuis, F. J. M. (2020). Is silicon a panacea for alleviating drought and salt stress in crops? *Frontiers in Plant Science*, 11(August), 1221. <https://doi.org/10.3389/fpls.2020.01221>
- Thorne, S. J., Stirnberg, P. M., Hartley, S. E., & Maathuis, F. J. M. (2022). The ability of silicon fertilisation to alleviate salinity stress in Rice is critically dependent on cultivar. *Rice*, 15(1), 8. <https://doi.org/10.1186/s12284-022-00555-7>
- Tubana, B. S., Babu, T., & Datnoff, L. E. (2016). A review of silicon in soils and plants and its role in US agriculture: History and future perspectives. *Soil Science*, 181(9–10), 393–411. <https://doi.org/10.1097/SS.0000000000000179>
- Violle, C., Garnier, E., Lecoœur, J., Roumet, C., Podgeur, C., Blanchard, A., & Navas, M. L. (2009). Competition, traits and resource depletion in plant communities. *Oecologia*, 160(4), 747–755. <https://doi.org/10.1007/s00442-009-1333-x>
- Wu, X., Yu, Y., Baerson, S. R., Song, Y., Liang, G., Ding, C., Niu, J., Pan, Z., & Zeng, R. (2017). Interactions between nitrogen and silicon in rice and their effects on resistance toward the brown planthopper *Nilaparvata lugens*. *Frontiers in Plant Science*, 8(January), 28. <https://doi.org/10.3389/fpls.2017.00028>
- Xu, D., Gao, T., Fang, X., Bu, H., Li, Q., Wang, X., & Zhang, R. (2020). Silicon addition improves plant productivity and soil nutrient availability without changing the grass:Legume ratio response to N fertilisation. *Scientific Reports*, 10, 10295. <https://doi.org/10.1038/s41598-020-67333-7>
- Yamamoto, T., Nakamura, A., Iwai, H., Ishii, T., Ma, J. F., Yokoyama, R., Nishitani, K., Satoh, S., & Furukawa, J. (2012). Effect of silicon deficiency on secondary cell wall synthesis in rice leaf. *Journal of Plant Research*, 125(6), 771–779. <https://doi.org/10.1007/s10265-012-0489-3>
- Yan, G., Nikolic, M., Ye, M., Xiao, Z., & Liang, Y. (2018). Silicon acquisition and accumulation in plant and its significance for agriculture. *Journal of Integrative Agriculture*, 17(10), 2138–2150. [https://doi.org/10.1016/S2095-3119\(18\)62037-4](https://doi.org/10.1016/S2095-3119(18)62037-4)
- Yenish, J. P., & Young, F. L. (2004). Winter wheat competition against jointed goatgrass (*Aegilops cylindrica*) as influenced by wheat plant height, seeding rate, and seed size. *Weed Science*, 52(6), 996–1001. <https://doi.org/10.1614/ws-04-006r>

- Zanão Júnior, L. A., Fontes, R. L. F., Neves, J. C. L., Korndörfer, G. H., & de Ávila, V. T. (2010). Rice grown in nutrient solution with doses of manganese and silicon. *Revista Brasileira de Ciência do Solo*, 34(5), 1629–1639. <https://doi.org/10.1590/S0100-06832010000500016>
- Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer-Verlag New York. <https://doi.org/10.1007/978-0-387-87458-6>

How to cite this article: de Tombeur, F., Lemoine, T., Violle, C., Fréville, H., Thorne, S. J., Hartley, S. E., Lambers, H., & Fort, F. (2022). Nitrogen availability and plant-plant interactions drive leaf silicon concentration in wheat genotypes. *Functional Ecology*, 36, 2833–2844. <https://doi.org/10.1111/1365-2435.14170>

SUPPORTING INFORMATION

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Résumé

La domestication a conduit à de profonds changements phénotypiques des espèces cultivées, amenant à l'émergence de « syndromes de domestication ». L'adaptation de ces espèces aux conditions de culture issues de la Révolution Verte (peuplement monospécifique/monogénotypique, forte densité, fort apport d'intrants), a abouti à un surinvestissement des individus dans la compétition pour les ressources, au détriment de la productivité du groupe. Bien que la compétition intraspécifique dans les cultures soit un sujet central pour les sélectionneurs et les agronomes depuis le milieu du XX^e siècle, l'évolution de l'aptitude à la compétition chez les espèces cultivées est encore mal connue. L'objectif général de cette thèse est d'évaluer comment la domestication et la sélection moderne ont modulé les stratégies écologiques et l'aptitude à la compétition du blé dur. En mobilisant les concepts et les méthodes de l'écologie fonctionnelle, nous avons caractérisé des traits aériens et racinaires chez des lignées issues d'une population de pré-sélection, et chez un panel de génotypes issu d'une série de domestication allant du compartiment sauvage au compartiment élite. Ce travail a permis de montrer que i) l'espace phénotypique du blé dur était structuré par les mêmes compromis que ceux décrits au niveau interspécifique, ii) les formes domestiquées étaient plus performantes en compétition que leurs ancêtres sauvages, et cela malgré une plus faible plasticité des traits, et, iii) la réponse de la biomasse à l'augmentation de la densité était similaire entre les différents compartiments de la série de domestication du blé dur, et s'expliquerait notamment par de mêmes contraintes allométriques entre compartiments. Cette thèse permet d'améliorer notre compréhension des effets de la domestication et de la sélection moderne sur l'écologie d'une espèce de grande culture. L'étude des stratégies écologiques et des interactions plante-plante au sein des espèces cultivées ouvre des opportunités intéressantes pour l'amélioration variétale et des pistes pour l'amélioration de la performance des cultures.

Abstract

Domestication has led to profound phenotypic changes in cultivated species, resulting in the emergence of "domestication syndromes". The adaptation of these species to the growing conditions stemming from the Green Revolution (monospecific/monogenotypic populations, high densities, high input levels) has led to an overinvestment of individuals in competition for resources, at the expense of group productivity. Although intraspecific competition in crops has been a central topic for breeders and agronomists since the mid-twentieth century, the evolution of competitive ability in cultivated species is still poorly understood. The overall objective of this thesis is to assess how domestication and modern breeding have shaped the ecological strategies and competitive ability of durum wheat. Using concepts and methods of functional ecology, we characterized aerial and root traits in lines derived from a pre-selection population, as well as in a panel of genotypes from a series of domestications ranging from the wild compartment to the elite compartment. This work demonstrated that i) the phenotypic space of durum wheat was structured by the same compromises as those described at the interspecific level, ii) domesticated forms outperformed their wild ancestors in competition, despite lower trait plasticity, and iii) the biomass response to increased density was similar across different compartments of the durum wheat domestication series, likely due to shared allometric constraints among compartments. This thesis enhances our understanding of the effects of domestication and modern breeding on the ecology of a major crop species. The study of ecological strategies and plant-plant interactions within cultivated species opens up interesting opportunities for varietal improvement and avenues for improving crop performance.