Alicia Gómez Fernández
Tesis doctoral

Plant size variation in crops: Causes, mechanisms and consequences

Universidad Rey Juan Carlos

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INDEX

RESUMEN ABREVIADO

Antecedentes

Existe un interés general por mejorar el rendimiento y la adaptación de los cultivos, debido a la inseguridad alimentaria que plantea una población humana en constante crecimiento y las predicciones futuras de cambio global. El rendimiento de los cultivos ha experimentado un crecimiento espectacular gracias al desarrollo agronómico y a los avances genéticos en el fitomejoramiento. Los rasgos fisiológicos son clave para el crecimiento de las plantas y el rendimiento de los cultivos, y en las últimas décadas, han sido el objetivo para lograr rendimientos más altos y/o más eficientes en el uso de los recursos. Hasta ahora, sin embargo, los rasgos fisiológicos no se han relacionado en general con los aumentos de la productividad agrícola tras la domesticación de las plantas. Curiosamente, los rasgos relacionados con el tamaño, como el tamaño de las semillas, las hojas y la planta, parecen haber aumentado a lo largo de la evolución bajo cultivo, pero se desconoce si estos cambios en el tamaño subyacen a los aumentos en el rendimiento de los cultivos. En general, necesitamos estudios comparativos más amplios que examinen cómo han cambiado la fisiología y el crecimiento de las plantas durante la evolución de los cultivos, así como una mejor comprensión mecanicista de las causas de la variación en el tamaño de las plantas y el rendimiento de los cultivos.

Los intentos anteriores de explicar los aumentos en el tamaño de las plantas y el rendimiento de los cultivos partiendo de la fisiología han aportado sólo conocimientos limitados. Esta laguna de conocimiento puede deberse en parte a la falta de experimentos de crecimiento detallados y a los diferentes enfoques que existen para medir, calcular y estandarizar el crecimiento, que limitan las comparaciones entre estudios. Desconocemos también cómo han evolucionado los rasgos fisiológicos durante la domesticación y la mejora moderna, ya que los estudios suelen incluir plantas domesticadas sin distinguir entre ‘landraces’ (es decir, las primeras domesticadas) y variedades mejoradas. Hay pruebas de que las especies agrícolas tienen tasas fotosintéticas más altas que las especies silvestres. Sin embargo, no está claro si este perfil adquisitivo es consecuencia de (i) la selección temprana de plantas silvestres de rápido crecimiento por parte de los primeros agricultores antes de que comenzara la domesticación; o (ii) su posterior evolución bajo cultivo. Así pues, también debemos distinguir a los progenitores de los cultivos de otras

especies silvestres que no fueron domesticadas para desentrañar los efectos de la selección temprana. Por último, sabemos que el proceso de domesticación de cada cultivo tiene sus propias particularidades, debido a las complejas interacciones entre factores sociales, ambientales y biológicos. Estas peculiaridades incluyen, entre otras, la filogenia, la antigüedad del cultivo, el órgano cosechado, y la procedencia geográfica de los progenitores silvestres de los cultivos. Cómo ha influido la diversidad de historias y orígenes de domesticación en la evolución de los rasgos de los cultivos es también una cuestión sin resolver.

La masa de semillas y el tamaño de las plantas han aumentado generalmente durante la evolución bajo cultivo. Se ha sugerido que el mayor tamaño de las semillas promueve la germinación y el establecimiento, la competencia por la luz y, en última instancia, el tamaño final de la planta gracias a la ventaja inicial en el crecimiento y a efectos acumulativos durante la ontogenia. La ontogenia de las plantas abarca diferentes fases de desarrollo, desde la plántula hasta la senescencia, pasando por las fases juvenil y madura. Las semillas más pesadas suelen germinar antes y se convierten en plántulas más grandes, con órganos a su vez más grandes. Sin embargo, se desconoce si la ventaja inicial de las semillas más pesadas se mantiene a lo largo de la ontogenia y conduce finalmente a plantas maduras grandes. Además de las semillas, la variación del tamaño de la planta durante la ontogenia también depende de las dinámicas de crecimiento, que incluyen las tasas de crecimiento y la duración del crecimiento vegetativo. Las tasas de crecimiento se miden normalmente como tasa de crecimiento relativo (RGR, el aumento de biomasa por unidad de biomasa preexistente y por unidad de tiempo) y la duración del crecimiento vegetativo, como el número de días hasta la floración. La RGR a su vez puede descomponerse en tres componentes subyacentes que reflejan la eficiencia fotosintética (tasa de asimilación neta), la asignación de biomasa (proporción de masa foliar) y los costes de biomasa por área foliar (área foliar específica). Sin embargo, faltan pruebas sobre el papel relativo del tamaño de la semilla, la RGR y sus componentes, y los rasgos fenológicos a la hora de explicar la variación del tamaño de la planta. Por lo tanto, necesitamos experimentos de crecimiento rigurosos en los que diversos tamaños iniciales, tasas de crecimiento y patrones fenológicos sean tenidos en cuenta para explicar la variación en el tamaño de las plantas y el rendimiento de los cultivos.

Objetivos

El principal objetivo de esta tesis es investigar los efectos de las distintas etapas de la evolución de los cultivos (es decir, la selección de progenitores silvestres, la domesticación y la mejora moderna) sobre el tamaño y la fisiología de las plantas, así como comprender los mecanismos subyacentes al aumento del tamaño de las plantas y rendimiento de los cultivos. Esta tesis además explora las estrategias ecológicas de los cultivos, y aborda las consecuencias de la evolución de los cultivos para los futuros programas de mejora y los orígenes de la agricultura. En este contexto, los objetivos específicos de la tesis son:

1. Evaluar la importancia de la selección temprana de progenitores silvestres *vs*. la evolución bajo cultivo para la prevalencia de rasgos ecofisiológicos adquisitivos en los cultivos (Capítulo 1).
2. Explorar si la selección temprana, la domesticación y la mejora moderna han provocado que la fisiología de los cultivos evolucione más allá de los límites fisiológicos observados en la naturaleza (Capítulo 1).
3. Comprender cómo han evolucionado la RGR y sus componentes durante la domesticación y la mejora moderna, comparando las tasas de crecimiento entre progenitores, 'landraces' y variedades mejoradas de 19 cultivos herbáceos (Capítulo 2).
4. Investigar los efectos de la filogenia, el origen geográfico y la historia de domesticación de 19 cultivos herbáceos sobre los cambios en la RGR y sus componentes durante la domesticación y la mejora moderna (Capítulo 2).
5. Medir la importancia relativa de la masa de semilla, la RGR y la duración del crecimiento vegetativo a la hora de explicar las variaciones en el tamaño final de la planta, teniendo en cuenta los cambios ontogenéticos y las correlaciones entre rasgos (Capítulo 3).
6. Examinar las consecuencias de los cambios en los rasgos morfológicos, fisiológicos y fenológicos para el aumento de tamaño de las plantas y del rendimiento de los cultivos durante la domesticación y la mejora moderna (Capítulo 3).

Metodología

Se realizaron tres experimentos de crecimiento para abordar los objetivos específicos de la tesis. El primer experimento, denominado en lo sucesivo *experimento ecofisiológico*,

investigó los efectos de la domesticación y la mejora moderna en la ecofisiología de 11 cultivos herbáceos. El segundo experimento, denominado *experimento intensivo*, examinó en detalle la variación de la tasa de crecimiento durante la evolución del trigo duro (*Triticum turgidum* L.). El último, el *experimento extensivo*, exploró la evolución de la masa de las semillas y las dinámicas de crecimiento tras la domesticación y la mejora moderna, así como sus consecuencias sobre el tamaño de las plantas y el rendimiento de los cultivos en un conjunto diverso de 18 especies de cultivo. En ambos experimentos cultivamos múltiples accesiones de progenitores silvestres, 'landraces' y variedades mejoradas de cada cultivo. Al comparar las 'landraces' con sus progenitores silvestres y con las variedades mejoradas, abordamos los efectos de la domesticación y la mejora moderna, respectivamente. Por último, la tesis se apoya en la recopilación de datos de bases de datos globales.

Resultados

En el Capítulo 1, situamos los rasgos ecofisiológicos de los progenitores silvestres de los cultivos en el contexto de la diversidad botánica mundial. Además, exploramos si la selección de progenitores silvestres, la domesticación y la mejora moderna han reducido la diversidad de rasgos y desplazado a los cultivos más allá de los límites fenotípicos de las especies silvestres. Para ello, recopilamos un conjunto de datos sobre rasgos ecofisiológicos de 1.148 hierbas anuales, incluyendo plantas domesticadas, progenitores de cultivos y especies silvestres, y realizamos el *experimento ecofisiológico* para examinar en profundidad los efectos de la domesticación y la posterior mejora en la ecofisiología de los cultivos. Nuestros resultados mostraron que los rasgos ecofisiológicos de los cultivos no han cambiado durante y después de la domesticación, e indicaron que su hábito de crecimiento rápido ya estaba presente en sus progenitores silvestres. También descubrimos que las tres etapas de la evolución de los cultivos no han dado lugar a nuevas combinaciones de rasgos, sino a una menor diversidad fenotípica en los cultivos en comparación con las plantas silvestres.

En el Capítulo 2, examinamos hasta qué punto la domesticación y la mejora moderns han influido en la RGR y sus componentes, basándonos en el *experimento intensivo* y *extensivo*. Utilizando mediciones no destructivas y modelos de crecimiento no lineales, obtuvimos la RGR y sus componentes a un tamaño de planta común. También investigamos las diferencias entre taxones, recopilando datos sobre el origen y la historia

de domesticación de cada cultivo. Descubrimos que las reacciones de la RGR y sus componentes a la domesticación y la mejora moderna son diversas entre los cultivos. Estas diversas respuestas dependen del tipo de cultivo, del clima en el lugar de origen del cultivo y de la posición filogenética. Curiosamente, la importancia de los componentes del RGR difiere según el órgano de la planta bajo selección, y la domesticación ha modificado los componentes del RGR en direcciones opuestas, lo que puede dar lugar a que no haya efectos netos de la domesticación sobre el RGR.

Por último, en el Capítulo 3, exploramos cómo la semilla, el crecimiento y la fenología interactúan durante la ontogenia para explicar las variaciones en el tamaño final de los cultivos herbáceos anuales. Además, investigamos la evolución del tamaño de las plantas y sus impulsores tras la domesticación y mejora moderna, y cómo dicha evolución ha influido en el rendimiento de los cultivos. En el *experimento extensivo*, medimos la masa de semillas, la tasa de crecimiento relativo y la duración del crecimiento vegetativo, junto con el rendimiento reproductivo y el tamaño de la planta en tres etapas de desarrollo: plántula, juvenil y madura. Descubrimos que la masa de semillas y la duración de la vida vegetativa contribuyen más que las tasas de crecimiento a la variación en el tamaño de la planta madura y su rendimiento. Los cultivos tienen semillas más grandes, pero no crecen más rápido ni durante más tiempo que sus progenitores silvestres. Así pues, la evolución bajo cultivo ha aumentado el tamaño de las plantas gracias a la selección de semillas pesadas, cuyos efectos se trasmiten en cascada a lo largo de la ontogenia. Sin embargo, observamos que ninguno de los rasgos considerados en la tesis explica el alto rendimiento de los cultivos modernos, lo que abre un nuevo horizonte de investigación.

Conclusiones

1. Los cultivos y sus progenitores silvestres comparten rasgos similares en cuanto al uso de recursos, teniendo todos ellos mayor cantidad de nitrógeno foliar, fotosíntesis, conductancia, transpiración y hojas más blandas que las especies silvestres que nunca fueron domesticadas. Sin embargo, estos rasgos no han cambiado sistemáticamente durante y después de la domesticación. Otros atributos relacionados con la capacidad competitiva (como el tamaño de la planta y la masa de semillas) sí difieren entre las plantas domesticadas y sus progenitoras, lo que sugiere que la capacidad de superar a otras especies (mediante un mayor tamaño) ha sido un factor más importante en la selección agrícola que la adquisición de recursos y el crecimiento.

2. La domesticación comenzó con especies adquisitivas y fisiológicamente menos diversas, es decir, los progenitores silvestres de los cultivos, lo que puede haber impedido mejoras posteriores en la ecofisiología de los cultivos. Las limitaciones a la evolución posterior pueden deberse a la menor diversidad fenotípica, a las compensaciones entre rasgos a distintos niveles de organización, y a los factores limitantes de la capacidad fotosintética. Así pues, la elección inicial de especies silvestres por parte de los primeros agricultores afecta a la evolución de los cultivos.
3. La fisiología adquisitiva de los progenitores silvestres de los cultivos podría reflejar su preadaptación a los primeros entornos antropogénicos ricos en agua y nutrientes y/o ser una consecuencia indirecta de la selección de especies silvestres palatables y nutritivas.
4. Los cultivos no tienen rasgos ecofisiológicos únicos que los diferencien de las especies silvestres, sino que sus parientes silvestres ocupan el extremo adquisitivo del espacio de rasgos y los rasgos ecofisiológicos no han cambiado consistentemente tras la domesticación.
5. La RGR está impulsada principalmente por el componente fisiológico y no ha aumentado de forma consistente tras la domesticación, en consonancia con las respuestas de los rasgos ecofisiológicos foliares.
6. Las reacciones de los tres componentes de la RGR –fisiología, alocación y morfología– a la domesticación son diversas, y pueden anularse entre sí cuando se combinan en un proceso a nivel de toda la planta como la RGR.
7. Entre los cultivos, las respuestas de la RGR y sus componentes a la domesticación dependen de factores ambientales (como el clima en el origen geográfico de los cultivos) y de la posición filogenética, y cambian notablemente con el órgano de la planta bajo selección.
8. Los progenitores silvestres y/o los ‘landraces’ albergan una mayor diversidad de rasgos de crecimiento que las variedades modernas. Por lo tanto, la diversidad intraespecífica dentro de las especies en los rasgos de crecimiento ha disminuido durante la evolución de los cultivos.
9. Las plantas con semillas grandes muestran RGRs bajas, incluso cuando las RGRs se miden con plantas de tamaño similar. Es posible que un aumento adicional de las RGRs no mejore el rendimiento de los cultivos debido a las compensaciones con otros rasgos relevantes (p. ej., el tamaño de la semilla y/o la inversión en defensa).

10. La tasa de crecimiento es menos importante que el tamaño de la semilla y la duración del crecimiento vegetativo a la hora de explicar la variación en el tamaño de la planta madura, apoyando el eje de variación tamaño de la planta–tamaño de la semilla, pero también destacando el papel de la fenología como un impulsor clave del tamaño de la planta.
11. La ontogenia importa: La fuerte relación positiva entre la masa de la semilla y el tamaño de la planta en la fase de plántula implica que las plantas con tamaños iniciales mayores se convertirán más tarde en plantas maduras más grandes, a pesar de sus menores RGRs.
12. La masa de la semilla y la duración del crecimiento son más importante que la RGR para aumentar el rendimiento de los cultivos, y podría ser una de las razones por las que se seleccionaron genotipos de semillas grandes durante la domesticación. Los altos rendimientos de los cultivos modernos también se explican por otros rasgos no considerados en esta tesis, lo que hace necesario explorar otros rasgos impulsores de la variación en los rendimientos de los cultivos.
13. El tamaño de las semillas y las dinámicas de crecimiento están fuertemente coordinadas con el tamaño de la planta, a pesar de los cambios en las medias de los rasgos durante la evolución de los cultivos, probablemente debido a la alta contribución de todos ellos a las tasas vitales (*i.e.* crecimiento, supervivencia y reproducción).

ABSTRACT

Background

There is a general interest in improving the performance and adaptation of crops, given the global food insecurity caused by an ever-growing human population and a globally changing environment. Crop yields experienced spectacular growth during evolution under cultivation thanks to agronomic developments and genetic advances in plant breeding. Physiological traits are key to plant growth and crop yields, and have been targets for achieving higher and/or more resource-use-efficient crop yields in recent decades. So far, however, physiological traits have not generally been linked to the increases in agricultural productivity following plant domestication. Interestingly, size-related traits such as seed, leaf and whole-plant size appear to have increased over the course of evolution under cultivation, but it is unknown whether these changes in size underlie increases in crop yields. In general, we need more extensive comparative studies examining how plant physiology and growth have changed during crop evolution as well as a better mechanistic understanding of the causes of variation in plant size and crop yields.

Previous attempts to explain increases in plant size and crop yields on the basis of physiology have provided only limited insights. This knowledge gap may be due in part to the lack of detailed growth experiments, and the diverse approaches used to measuring, calculating and standardising growth, which limit comparisons between studies. We also unknown how physiological traits have evolved during initial domestication and subsequent plant breeding, as studies usually include domesticated species without distinguishing between landraces (*i.e.* early domesticates) and improved cultivars. There is evidence that crop species have higher photosynthetic rates than wild species. However, it is unclear whether this acquisitive profile is a consequence of (i) the early selection of fast-growing wild plants by proto-farmers before domestication began; or (ii) their later evolution under cultivation. Thus, we also need to distinguish crops' progenitors from other wild species that were not domesticated to decipher the effects of early human selection. Finally, we know that the domestication process of each crop has its own peculiarities, due to the complex interactions between social, environmental and biological factors. These peculiarities include, among others, the phylogeny, the crop

antiquity, the organ harvested, and the climatic niche of crops' wild progenitors. How diversity in domestication histories and origins have influenced the evolution of crop traits is also an open research question.

Seed mass and plant size have generally increased during evolution under cultivation. Larger seed sizes have been suggested to promote germination and establishment, competition for light, and ultimately final plant size through a head-start advantage in growth and cumulative effects during ontogeny. Plant ontogeny encompasses different developmental stages, from seedling through juvenile and mature stages to senescence. Heavier seeds often germinate earlier and grow into larger seedlings with larger organs. However, it is unknown whether the early advantage of heavier seeds continues throughout ontogeny, and eventually leads to larger mature plants. In addition to seeds, variation in plant size during ontogeny also depends on growth dynamics, which include growth rates and duration of vegetative growth. Growth rates are usually measured as relative growth rate (RGR, the increase in biomass per unit of pre-existing biomass and per unit time) and the duration of vegetative growth as the number of days to flowering. RGR can be decomposed into three underlying components reflecting photosynthetic efficiency (net assimilation rate), biomass allocation (leaf mass ratio), and biomass costs of leaf area (specific leaf area). However, evidence is lacking on the relative roles of seed size, RGR and its components, and phenological traits on accounting for variation in plant size. Therefore, we need rigorous growth experiments in which combinations of diverse initial sizes, growth rates and phenological patterns are taken into account to explain variation in plant size and crop yields.

Objectives

The main objective of this thesis is to investigate the effects of the different stages of crop evolution (*i.e.* selection of wild progenitors, domestication and improvement) on plant size and physiology, and to understand the mechanisms underlying increases in plant size and crop yields. This thesis also explores the ecological strategies of crops and addresses the consequences of crop evolution for future breeding programmes and the origins of agriculture. In this context, the specific objectives of the thesis are:

1. To assess the importance of early human selection of crops' wild progenitors *vs.* evolution under cultivation for the prevalence of acquisitive ecophysiological traits in crops (Chapter 1).

2. To explore whether early human selection, domestication and improvement have caused crop physiology to shift beyond the physiological limits observed in the wild (Chapter 1).
3. To understand how RGR and its components have evolved during domestication and modern plant breeding by comparing the growth rates among progenitor, landrace and improved accessions of 19 herbaceous crops (Chapter 2).
4. To investigate the effects of phylogeny, geographical origin and domestication history of 19 herbaceous crops on changes in RGR and its components during domestication and modern plant breeding (Chapter 2).
5. To measure the relative importance of seed mass, RGR and duration of vegetative growth to explain variations in mature plant size, taking into account ontogenetic changes and trait correlations (Chapter 3).
6. To examine the consequences of changes in morphological, physiological and phenological traits for increases in plant size and crop yields during domestication and modern plant breeding (Chapter 3).

Methodology

Three controlled growth experiments were conducted to address the specific objectives of the thesis. The first experiment, hereafter referred to as the *ecophysiological experiment*, investigated the effects of domestication and improvement on the ecophysiology of 11 herbaceous crops. The second experiment, called the *intensive experiment*, examined in detail the variation in growth rate during the evolution of durum wheat (*Triticum turgidum* L.). The last experiment, the *extensive experiment*, explored the evolution of seed mass and growth dynamics after domestication and further modern breeding, and their consequences on plant size and crop yields in a diverse set of 18 crops. In both experiments, we grew multiple accessions of wild progenitors, landraces, and improved cultivars of each crop. By comparing landraces with their wild progenitors and with improved cultivars, we addressed the effects of domestication and modern breeding, respectively. Finally, the thesis is supported by data compilation from global databases.

Results

In Chapter 1, we placed the ecophysiological traits of crops' wild progenitors in the context of global botanical diversity. In addition, we explored whether selection of wild

progenitors, domestication, and improvement have reduced trait diversity and shifted crops beyond the phenotypic boundaries of wild species. To this end, we compiled a global dataset on relevant ecophysiological traits of 1,148 annual herbs, including domesticates, crops' wild progenitors and wild species, and conducted the *ecophysiological experiment* to examine in-depth the effects of domestication and improvement on crop ecophysiology. Our results showed that ecophysiological traits of crops have not been changed during and after domestication, and indicated that their fast-growth habit was already present in their wild progenitors. We also found that the three stages of crop evolution have not led to new trait combinations, but to lower phenotypic diversity in crops compared to wild plants.

In Chapter 2, we examined the extent to which domestication and modern plant breeding have impacted RGR and its components, based on the *intensive* and *extensive experiments*. Using nondestructive measurements and nonlinear growth models, we obtained the RGR and its components at a common plant size. We also investigated differences among taxa, by compiling data on the origin and domestication history of each crop. We found that the reactions of RGR and its components to domestication and improvement are diverse among crops. These diverse responses depend on the type of crop, the climate at crop origin, and the phylogenetic position. Interestingly, the importance of RGR components differs depending on the plant organ under selection, and domestication have changed RGR components in opposite directions, which may result in no net effects of domestication on RGR.

Finally, in Chapter 3, we explored how seed, growth and lifespan interact during ontogeny to explain variations in the mature plant size. Additionally, we investigated the evolution of plant size and its drivers after plant domestication and improvement, and how that evolution has influenced crop yields. In the *extensive experiment*, we measured seed mass, RGR and vegetative lifespan, together with reproductive output and plant size at three developmental stages: seedling, juvenile and mature. We found that seed mass and vegetative lifespan contribute more than growth rates to variation in mature plant size and yield. Crops have larger seeds but do not grow faster or for longer time spans than their wild progenitors. Thus, evolution under cultivation have increased plant size only through the heavy-seed causal pathway, via cascading effects throughout ontogeny.

However, we observed that none of the traits considered in this thesis explains the high yields of modern crops, which opens up a new focus of research.

Conclusions

1. Crops and their wild progenitors share similar resource-use traits, all having higher leaf nitrogen, photosynthesis, conductance, transpiration, and softer leaves than wild species that were never domesticated. However, these traits have not consistently changed during and after domestication. Other attributes related to competitive ability (such as plant size and seed mass) do differ between domesticated and progenitor plants, suggesting that the ability to outcompete other species (through larger size) has been a more important factor in agricultural selection than resource acquisition and growth.
2. Domestication began with acquisitive, and physiologically less diverse species, *i.e.* crops´ wild progenitors, which may have prevented further improvements in crop ecophysiology. Constraints on further evolution may be due to the lower phenotypic diversity, trade-offs between plant traits at different organizational levels, and limiting factors of photosynthetic capacity. Thus, the initial choice of wild species by proto-farmers affects crop evolution.
3. The acquisitive physiology of crops' wild progenitors could reflect their pre-adaptation to early anthropogenic water- and nutrient-rich environments and/or be an indirect consequence of the selection of palatable and nutritious wild species.
4. Crops do not have unique ecophysiological traits that distinguished them from wild species – instead, their wild progenitors occupy the acquisitive end of the trait space and ecophysiological traits have not consistently changed after domestication.
5. RGR is mainly driven by the physiological component and has not increased consistently after domestication, in line with reactions of leaf ecophysiolofical traits.
6. The reactions of the three components of RGR –physiology, allocation and morphology– to domestication are diverse, and can cancel each other out when combined into a whole-plant level process such as RGR.
7. Among crops, the responses of RGR and its components to domestication depend on environmental factors (such as climate in the geographical origin of crops) and phylogenetic position, and change markedly with the plant organ under selection.
8. Wild progenitors and/or landraces harbour a greater diversity in growth traits than

modern cultivars. Therefore, intraspecific diversity within species in growth traits has decreased during crop evolution.

9. Plants with large seeds display low RGRs, even when RGRs are measured at similar plant sizes. Further increases in RGRs may not improve crop yields because of trade-offs with other relevant traits (*e.g.* seed size and or investment in defence).
10. Growth rate is less important than seed size and duration of vegetative growth in explaining variation in mature plant size, supporting the plant size–seed size axis of variation, but also highlighting the role of phenology as a key driver of plant size.
11. Ontogeny matters: The strong positive relationship between seed mass and plant size at the seedling stage implies that plants with larger initial sizes will later develop into larger mature plants, despite their lower RGRs.
12. Seed mass and duration of growth is more important than RGR for increasing crop yield and could be one of the reasons why large-seeded genotypes have been selected during domestication. The high yields of modern crops are also explained by other traits not considered in this thesis, which claims for exploring other drivers of variation in crop yields.
13. Seed mass and growth dynamics are highly functionally coordinated with plant size, despite shifts in trait means during crop evolution, probably due to their high joint contribution to vital rates (*i.e.* growth, survival and reproduction).

GENERAL INTRODUCTION AND AIMS

Background

Origins of agricultural crops

The development of **agriculture** is generally regarded as one of the defining moments in the evolution of humankind (Diamond, 2002). It first took place just over 12,000 – 11,000 years ago (ya) at the beginning of the **Neolithic** period (Fuller *et al.*, 2014). This revolutionary event completely changed the diets, lifestyles and structure of human societies, mostly by turning people into food-producers and settlers (Rindos, 2013). It was developed independently by several human cultures in various parts of the word (Asia, Africa, Mesoamerica, South America, Eastern North America, and New Guinea; (Gepts, 2004; Brown *et al.*, 2009; Price & Bar-Yosef, 2011; Gopher *et al.*, 2021). The causes for the onset of agriculture, the timing, the number of geographical origins and the rates of transition to agriculture are currently under active debate (Larson *et al.*, 2014; Abbo & Gopher, 2017; Gopher *et al.*, 2021). Nonetheless, there is good evidence that **climate change** was of great importance for the adoption of agriculture, at least by Near Eastern societies (Wright *et al.*, 2003). Sudden and severe climate changes during the Younger Dryas had enormous impacts on the type and distribution of plants and animals (Hillman *et al.*, 2001). As in previous ice ages, many temperate and subtropical forests were replaced by savannahs and prairie-like ecosystems (Mayle & Power, 2008). These climatic events forced certain groups of people to switch to alternative food sources and rely on a more limited number of plants. The initial stimulus to exploit the seeds of cereals and legumes (*i.e.* the first **founder crops**) was thus a combination of a general lack of animals and fruits and the relative abundance of herbs, which became more common due to the colder, drier climate (Murphy, 2007). However, alternative factors beyond climate change have been proposed as precursors to the origin of agriculture, such as human cognitive capacity, cultural complexity, demografic growth, and the availability of nutrient-rich and stable yielding plants (Braidwood, 1958; Cohen & Cohen, 1977; Abbo *et al.*, 2010).

In most places, the cultivation of crops was preceded by a long **pre-agricultural phase** of plant gathering (Smith, 2001). During this period, many geographically unconnected human groups began to collect and manage certain plant species for food

use, while still relying on a nomadic hunter-gatherer lifestyle (Harlan, 1967). For example, cereal grains were ground and processed to make them more edible and stored until food shortage periods, such as winter (Willcox & Stordeur, 2012). In addition, many centuries before cultivation, people had already developed harvesting tools to facilitate the collection of seeds from wild plant stands (Groman-Yaroslavski *et al.*, 2016). These pre-agricultural people also had detailed **botanical knowledge** about the surrounding plants, such as their nutritional quality and toxicity, their favourable habitats, their yield potential and stability, and their phenology (Forrester, 2013). In some cases, this cultural knowledge determined the selection of taxa that were later cultivated and domesticated (Whitlam *et al.*, 2018). During this pre-agricultural phase, plants engaged with humans would have experienced subtly different environments than in wild habitats. For example, some of the seeds collected would be accidentally dropped and grow near human settlements, which provided a fertile and disturbed environment (Zeven, 1973). P**roto-farmers** would have also selected those food plants that thrived, spread, and produced high yields in such human-altered habitats, while others would not (Zohary, 2004). This would have led to a gradual and unintentional **early selection** of plants that share certain phenotypical profiles adaptated to fertile, disturbed habitats (the so-called 'dump heap hypothesis'; first proposed by Engelbrecht (1916)). Alternative views on the conscious or unconscious selection of crops have been contributed by (Abbo et al., 2005; Spengler, 2022; Spengler & Mueller, 2019).

There is evidence of a gradual transition from this pre-agricultural phase to organised and deliberate cultivation and the consequent appearance of early domesticates. **Plant domestication** is an evolutionary process resulting from a mutualistic ecological interaction in which the fitness of one (plant) species is controlled by another (humans) so that the domesticator can obtain resources and/or services from the domesticate (Purugganan, 2022). Charles **Darwin** drew an analogy with plant and animal domestication for his theory of evolution by natural selection (Darwin, 1868). Another of the most influential early figures in the field of plant domestication was Alphonse **de Candolle**, who recognised that the key to understanding the domestication of crops lay in determining their places of origin (De Candolle, 1883). Following his footsteps, Nikolai **Vavilov** concluded that major crops originated from a few localised geographic regions, which he called '**centres of origin**' (Vavilov, 1992). The domestication of several crops took place independently in different centers of origin. For example, Asian

rice was domesticated in the Yangtze River valley (China) and in the in the Ganges plains (India), where spp. japonica and spp. indica originated respectively (Gross & Zhao, 2014). Following domestication, many crops spread beyond their initial centres of origin and achieved near-global distribution, promoting diverse, locally adapted varieties and influencing patterns of genetic diversity (**crop diversification;** (Meyer & Purugganan, 2013; Wang *et al.*, 2017). The search for high-yielding crops reached a milestone in the so-called **Green Revolution**. The Green Revolution began in the decade of the 1950s, when modern varieties of major cereals emerged as a result of breeding for **crop improvement** and adaptation to intensive agriculture, which allowed for greater health and life expectancy, but came at a very high long-term environmental and socio-economic costs (Evenson & Gollin, 2003; Pingali, 2012).

Crop biodiversity

Crops are diverse in terms of their phylogenetic, geographic and historical origins, their agricultural relevance and the ways in which they are used for agricultural purposes (such as food, textiles, medicines or ornamentals; (Milla & Osborne, 2021). Only a tiny fraction of the potential riches of the plant kingdom has ever been domesticated. It is estimated that there are a total of ca. 354,000 flowering plants worldwide compared to ca. 1,000 **crop species** (Purugganan, 2022; Qian *et al.*, 2022). About 80% of these crop species belong to only 17 botanical families (out of a total of 416 families), but these are distributed throughout the angiosperm tree, resulting in high **phylogenetic diversity** (Hufford *et al.*, 2019; Milla & Osborne, 2021). Within these crop species, rice, wheat, soya, and maize supply nearly two-thirds of human calorific needs (Ray *et al.*, 2013). Domestication of the different crop species did not occur at the same time. A group of eight species, including einkorn, emmer, barley, lentil, pea, chickpea, vetch, and flax form the major ancient crops, while brassicas are a much more recently domesticated group (Weiss & Zohary, 2011; Mabry *et al.*, 2021). Crops are thus not only distinguished by their place of origin, but also by their **antiquity** or time since they started to be domesticated (Milla & Osborne, 2021). Very different types of plants have been domesticated, such as grasses, legumes and forbs, representing different plant **functional groups**. There are also differences in the **organ under selection** (*i.e.* the organ harvested for agricultural use), with grain, leaf, fruit, and root crops, as well as crops such as the *Brassica* complex, where selection has generated varieties bred for different organs.

Despite their diverse evolutionary and geographic origins and their different domestication histories, certain fully-domesticated crops generally display similar domestication-related traits (Vavilov, 1922). The **domestication syndrome** is the evolutionary convergence of phenotypic traits, due to the existence of common selection pressures during evolution under cultivation (Hammer, 1984). **Classical traits** comprising this syndrome are as non-shattering seeds, large seeds, high yield, synchronous phenology, loos of seed dormancy, upright and compact growth habit, reduction in physical and chemical defences, and enlargement of harvestable organs (Meyer & Purugganan, 2013). Crops are dynamic entities, as the process of **evolution under cultivation** is an ongoing interaction between humans, plants and the environment, which still continues today (Gepts, 2004). Therefore, not all morphological, physiological and biochemical differences between crops and their wild ancestors can be attributed to the initial domestication. Indeed, it is widely accepted that there is a differentiation between phenotypic changes associated with domestication and those resulting from subsequent crop diversification and improvement (Yamasaki *et al.*, 2005; Burke *et al.*, 2007; Abbo *et al.*, 2012, 2014; Meyer & Purugganan, 2013).

Initial **domestication changes** are the phenotypic differences between the populations of the wild ancestors from which modern crops originated and the first domesticates managed by the Neolithic farmers. However, there are several plant traits (such as growth) that are undetectable in the archaeobotanical record, and others that are scarce or constrained to very few places (Abbo *et al.*, 2014). The best approximation to the original ancestral populations are the closest extant wild relatives of the crop (hereafter referred to as **wild progenitors**), while **landraces** (*i.e.* domesticated genotypes that have not been intensively bred in the last centuries) are so far the best proxy for the first domesticates. For many crop species, the progenitors are still unconfirmed or do not come from a single ancestral gene pool. For others, however, the wild progenitor assignment is supported by strong ecological, genomic and anthropological evidence. If current wild progenitor populations are geographically close to the centres of origin and have not suffered much gene introgression over time, they are a good proxy for the original ancestral populations. Finally, changes in plant traits during modern breeding (**improvement changes)** are the differences between the landraces and the **improved cultivars**, *i.e.* the last improved domesticated plants resulting from the Green Revolution breeding programmes. These two stages are good proxies for the improvement changes,

but it should be noted that the landraces that have persisted over the last century represent a small and biassed sample of the entire history of crop diversification.

Application of trait-based ecology to the study of domestication

The influence of very diverse factors on the origins of agriculture promotes its study from multiple angles and perspectives by disciplines such as archaeology, geology, climatology, genetics and agronomy, and more recently ecology (Milla 2015). Biologists have been trying to classify diversity for decades. The quantification of biodiversity has traditionally been based on the number of species, which primarily reflects the taxonomic facet of diversity. However, species are not only taxonomic units, but can also be described by their **phenotypic traits**. A trait is 'a measurable characteristic (morphological, phenological, physiological, behavioural, or cultural) of an individual organism that is measured at either the individual or other relevant level of organization' (Dawson *et al.*, 2021). Traits are at the core of **trait-based ecology**, disciple of ecology which aims to describe, synthesise and understand diversity from a phenotypic perspective at different organizational levels (Garnier *et al.*, 2016a; Chacón-Labella *et al.*, 2022). Each phenotypic trait does not evolve or vary independently of other traits, as there is often covariations and **trade-offs** between traits (Chapin III *et al.*, 1993; Reich *et al.*, 1997). The identification of such trait combinations and their recurrence among environments has led to the identification of a number of axes of trait variation representing different ecological strategies (Westoby *et al.*, 2002; Laughlin, 2014).

The concept of **ecological strategies** is based on the assumption that similar environments and types of ecological interactions exert similar selection forces on different species, leading to convergent phenotypic evolution (Craine, 2009). There are diverse strategies because there are trade-offs between traits, so that a particular combination of traits that is favourable in one environment may be unfavourable in another (Garnier *et al.*, 2016b). Among the most relevant and pioneering work in the field of ecological strategies is **Grime's CSR model** (Grime, 1974, 1977), which defines three primary strategies –Competitive (C), Stress tolerant (S) and Ruderal (R)– as a function of the interaction of two environmental factors: resource availability and disturbance. These strategies correspond respectively to plants that are found in environments: (1) where resource availability is high and the level of disturbance is low (competitors); (2) where both resource availability and the level of disturbance are low (stress-tolerators); or (3)

where both resource availability and the level of disturbance high (ruderals). Due to the form of the environmental space that can be occupied by plants, this model is triangular (Grime, 1974, 1979). Phenotypic traits can be used to locate species within this triangle, as plants selected under stressful conditions exhibit different traits than ruderal and competitive plants (Grime *et al.*, 1997; Grime & Pierce, 2012).

The ordination of species by their functional traits has led to the identification of the main **axes of plant trait variation**. Currently, there are two main axes of global trait variation: (1) plant resource economics (a trade-off between traits conferring rapid acquisition in productive habitats and efficient conservation of resources under unproductive conditions) and (2) the size of plants and plant organs (Díaz *et al.*, 2016). Diaz et al. (2016) found that the axis of plant resource economics is captured by traits linked to the '**leaf economics spectrum**' (LES), *i.e.* it runs from species with cheap, short-lived, 'acquisitive' leaves (low thickness, high nitrogen) to species with 'conservative' leaves (high thickness, low nitrogen) (Wright *et al.*, 2004; Reich, 2014). The other axis runs from short species, which tend to have small seeds and leaves, to tall species, which tend to have large seeds and leaves (Niklas, 2004). The selective forces acting on the traits of these two axes can be considered independent, and both axes have been proposed as key determinants of plant ecological strategies according to the CSR triangle (Pierce *et al.*, 2017). The **axis of plant resource economics** is associated with the gradient liking stress tolerants and ruderals (*i.e.* between S and R strategies), and the **axis of plant size**, which is orthogonal to the previous axis, is related to competitive ability of plants, plant longevity and dispersal capability (Moles, 2018).

Apart from the taxonomic and phenotypic facets of biodiversity, there is another one based on the **evolutionary relationships** between species. (Darwin, 1859) recognised that closely-related species, *i.e.* species that share a recent common ancestry, are usually ecologically and phenotypically more similar than distantly-related species. This is called 'trait phylogenetic conservatism' and refers to the tendency of species to preserve ancestral characteristics (Ackerly, 2009). The evolution of phenotypic traits may thus depend on the phylogenetic relatedness of species (Silvertown *et al.*, 1997). However, traits differ greatly in their degree of trait conservatism. For example, plant height is a poorly conserved trait, whereas seed mass shows a high **phylogenetic signal**, *i.e.* a statistical measure of the dependence among species' trait values due to their phylogenetic

relationships (Cavender-Bares et al. 2006). Evolutionary trait dependence may constrain (or facilitate) the change in traits related to domestication and improvement, thus obscuring the detection of trait convergence. **Phenotypic convergence** in crops is the independent evolution of the same phenotype in phylogenetically distinct species as a result of the existence of similar selection pressures (such as similar cultivation conditions, agricultural management practises, and human cultural preferences; (Purugganan, 2019).

Characterizing biodiversity by phenotypic traits can provide insight into the common selection pressures that have led to crops sharing certain phenotypic profiles, regardless their phylogenetic history. The process of evolution under cultivation involves the action of three selection forces operating simultaneously: natural selection, human selection and indirect selection (Milla *et al.*, 2015). **Natural selection** under cultivation operates to change the frequency of traits that promote differences in the fitness of crop populations, allowing adaptation to human-managed environments (Zohary, 2004). **Artificial selection** is the intentional human selection for traits of interest during initial domestication and subsequent improvement (Darwin, 1868). **Indirect selection** assumes that selection on trait X can lead to in indirect selection on trait(s) Y(s) because of the existence of correlations between traits (Gallais, 1984). For example, many traits related to biomass allocation, physiological rates and nutrient stoichiometry vary with plant size, as described by plant allometric theory (Qin *et al.*, 2012). This suggests that phenotypic changes during evolution under cultivation may be constrained by the existence of allometric, biophysical and ecophysiological constraints, pleiotropy or genetic effects, source-sink linkages, and trait interdependence (Gross & Beckage, 2012; Kluyver et al., 2017; Ledent, 1984).

Response of plant size and associated traits during evolution under cultivation

The major advances in a trait-based characterization of crops have occurred in reproductive traits (e.g. seed size, flowering time, yield), while less attention has been paid to vegetative development and growth. **Plant size** has generally increased over the course of evolution under cultivation, which can be attributed to the above-mentioned selection forces (Milla *et al.*, 2014). On the one hand, the shift from original wild habitats to human-managed environments (resource-rich, predictable ecosystems) may have promoted the evolution of crops towards **acquisitive, fast-growing traits**, and thus

toward larger sizes (Chapin III, 1980; Craine, 2009; Milla *et al.*, 2015). On the other hand, the intentional selection for high-yielding crops, might have indirectly selected for traits that drive yield and physiological performance, such as plant size (Milla & Matesanz, 2017). Therefore, it is reasonable to assume that domesticated plants may have evolved towards more acquisitive traits that allow them to adapt to cultivation conditions while raising their yields (Roucou *et al.*, 2017). However, there is a lack of comparative work assessing the evolution of growth and physiology under cultivation. It is also unknown the **proximal causal mechanisms** underlying such shifts in plant size and associated traits. We thus need more extensive comparative studies examining how physiology and growth rates have changed during crop evolution, as well as a better mechanistic understanding of the causes of variation in plant size and crop yields.

Previous attempts to explain increases in crop size on the basis of physiology or other traits that foster growth rates have provided only limited insights (Evans, 1993; Milla *et al.*, 2014; Preece *et al.*, 2017; Simpson *et al.*, 2017). This gap is partly due to the absence of detailed **growth experiments** over the entire plant lifespan and including multiple crop species and varieties within crops, as well as the diverse approaches to measuring, calculating and standardising growth (Paine *et al.*, 2012; Pommerening & Muszta, 2016). Moreover, there is lack of knowledge on how physiological traits have evolved during initial domestication and subsequent plant breeding, as studies usually include domesticated species without distinguishing between landraces and improved cultivars (see *e.g.* Delgado-Baquerizo et al., 2016; Martín-Robles et al., 2018; Matesanz & Milla, 2018). Furthermore, we have evidence that crops have higher photosynthetic rates than wild species (Nadal & Flexas, 2018; Huang *et al.*, 2022), but it is unclear whether this is a consequence of artificial selection or of early selection of crops' wild progenitors by proto-farmers in the pre-agricultural phase. Thus, we need to place focus on comparisons between crops, crops' wild progenitors and other wild species to disentangle the **effects before and after domestication** (Milla, 2023). Finally, we know that the domestication process of each crop has its own characteristics, as domestication depends on complex interactions between social, environmental and biological factors (Gepts, 2004). These peculiarities include, among others, phylogeny, crop antiquity, organ harvested, functional group, and the distribution and climatic niche of crops' wild progenitors (Milla & Osborne, 2021). How **diversity in domestication histories and**

origins have influenced the evolution of growth traits in crops is also an open research question.

Seed mass has also generally increased during evolution under cultivation and represents one of the classical domestication traits (Harlan *et al.*, 1973; Meyer & Purugganan, 2013; Kluyver *et al.*, 2017). Larger seed sizes have been suggested to promote establishment, competition for light, and ultimately plant size through a head start in growth and cumulative effects during ontogeny (Milla & Matesanz, 2017; Preece *et al.*, 2017). **Plant ontogeny** encompasses different developmental stages, from seedling through juvenile and mature stages to senescence (Gatsuk *et al.*, 1980). For example, heavier seeds often germinate earlier and grow into larger seedlings with larger organs (Moles & Westoby, 2004). However, it is unknown whether the early advantage of larger seeds continues throughout ontogeny, and eventually leads to taller and larger mature plants. Variation in plant size during ontogeny also depends on **growth dynamics**, which include growth rates and duration of vegetative growth (Violle *et al.*, 2007). Growth rates are usually measured as **relative growth rate** (RGR, the increase in biomass per unit of pre-existing biomass and per unit time; Blackman, 1919), and the **duration of vegetative growth** as the number of days to flowering. RGR in turn depends on photosynthetic rates and allocation and morphology of photosynthetically active tissues (RGR's underlying components; Poorter, 1990). However, evidence is lacking on the relative roles of seed size, biomass allocation patterns, leaf physiology and morphology, and phenological traits on accounting for variation in plant size. Therefore, we need rigorous growth experiments in which combinations of diverse initial sizes, growth rates and phenological patterns are considered and used to explain variation in trait-trait relationships and plant sizes.

Objectives

Evolution under cultivation has modified many morphological, physiological and phenological traits of crops, ultimately leading to generally larger plants. The **main objective** of this thesis was to assess the causal effects of early selection, domestication, and improvement on changes in plant size and size-related traits in crops. In addition, we aimed to understand the proximal mechanisms driving variation in plant size, and the consequences of changes in plant size and its drivers for crop yields, ecological strategies and future plant breeding. In this context, the **specific objectives** of the thesis were:

1. To assess the importance of early human selection of crops' wild progenitors *vs.* evolution under cultivation for the prevalence of acquisitive ecophysiological traits in crops (**Chapter 1**).
2. To explore whether early human selection, domestication and improvement have caused crops to evolve beyond the physiological limits of wild species on global scale (**Chapter 1**).
3. To understand how growth rates have evolved during domestication and modern plant breeding by comparing the evolution of growth rates among progenitor, landrace and improved accessions of 19 herbaceous crops (**Chapter 2**).
4. To investigate the effects of phylogeny, geographical origin and domestication history of 19 herbaceous crops on changes in growth rates during domestication and modern plant breeding (**Chapter 2**).
5. To measure the relative importance of seed mass, growth rate and duration of vegetative growth to explain variations in mature plant size, taking into account ontogenetic changes and trait correlations. (**Chapter 3**).
6. To examine the consequences of changes in morphological, physiological and phenological traits for increases in plant size and crop yields during domestication and modern plant breeding (**Chapter 3**).

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GENERAL METHODOLOGY

Three controlled growth experiments were conducted to address the specific objectives of the thesis. The first experiment, hereafter referred to as the *ecophysiological experiment*, investigated the effects of domestication and improvement on the ecophysiology of 11 herbaceous crops. The second experiment, called the *intensive experiment*, examined in detail the variation in growth rate during the evolution of durum wheat (*Triticum turgidum* L.). The last experiment, the *extensive experiment*, explored the evolution of seed mass and growth dynamics after domestication and further modern breeding, and their consequences on plant size and crop yields in a diverse set of 18 crops. Finally, the thesis is supported by relevant ecophysiological data collected from global databases.

The study system

In the experiments, we included a total of 19 annual herbaceous crops belonging to ten botanical families and four functional groups (Table 1). The three experiments had most of crop species in common to optimise the comparison of results. Our crop species selection attempted to represent a considerable portion of the diversity in domestication processes. For example, we considered crops that differ in when they were adopted for cultivation, from ancient crops that are more than 10,000 years old, such as wheat or lentils, to younger crops such as borage or tomatoes. We also included different types of crops in terms of their primary use (*e.g.* food, fibre and forage crops) and the organ under selection (*e.g.* fruit, seed and leaf crops) (Table 1). Finally, we look for phylogenetically diverse crops, covering a wide range of geographical origins. The diversity in domestication histories and crop origins justified the use of multiple crop species.

For each crop, we obtained seed lots from three domestication statuses: wild progenitor, landrace, and improved cultivar. We attempted to include a sufficient number of accessions/varieties for each domestication status and crop to perform robust statistical analyses and to capture diversity within crops without compromising the number of crop species considered. The total number of accessions used in the three experiments was 158. The identity of the putative wild progenitor of each crop was taken from the most up-to-date information available (the Crop Origins database; (Milla, 2020) (Table 1).

Since for many crop species the progenitors are still unconfirmed or not come from a single ancestral gene pool, we selected those wild species that provide the strongest support based on current ecological, genomic, and anthropological evidence, and different (and geographically diverse) wild accessions.

Table 1 Summary of the species included in the three experiments and their botanical family, functional group, time in cultivation (y.a.), main organ selected, geographic origin, and domestication status (P, wild progenitor; D, domesticate). Domesticate refers to accessions belonging to both local landraces and improved cultivars.

Crop	Botanical family	Functional group	Time in cultivation	Organ selected	Geographic origin	Dom. status	Species
Intensive experiment							
Emmer wheat	Poaceae	C_3 cereal	19,000	Seed	Palearctic	P	*Triticum turgidum* ssp. *dicoccoides*
						EL	*T. turgidum* ssp. *dicoccum*
Durum wheat	Poaceae	C_3 cereal	7,000	Seed	Palearctic	LL	*T. turgidum* ssp. *durum*
						I	*T. turgidum* ssp. *durum*
Ecophysiological and Extensive experiment							
Amaranth	Amaranthaceae	Forb	7,000	Seed	Nearctic	P	*Amaranthus hybridus*
						D	*A. cruentus*
Borage	Boraginaceae	Forb	850	Leaf	Paleartic	P	*Borago officinalis*
						D	*B. officinalis*
Cabbage	Brassicaceae	Forb	8,000	Leaf	Paleartic	P	*Brassica oleracea*
						D	*B. oleracea*
Faba bean	Fabaceae	Legume	10,500	Fruit	Paleartic	P	*Vicia narbonensis*
						D	*V. faba*
Lettuce	Asteraceae	Forb	7,500	Leaf	Paleartic	P	*Lactuca serriola*
						D	*L. sativa*
Pearl millet	Poaceae	C_4 cereal	5,000	Seed	Afrotropic	P	*Cenchrus americanus* *
						D	*C. americanus* *
Oat	Poaceae	C_3 cereal	10,000	Seed	Paleartic	P	*Avena sterilis*
						D	*A. sativa*
Okra	Malvaceae	Forb	3,150	Fruit	Indo Malay	P	*Abelmoschus tuberculatus*
						D	*A. esculentus*
Peanut	Fabaceae	Legume	9,000	Seed	Neotropic	P	*Arachis monticola*
						D	*A. hypogaea*
Tomato	Solanaceae	Forb	800	Fruit	Neotropic	P	*Solanum pimpinellifolium*
						D	*S. lycopersicum*
Sesame	Pedaliaceae	Forb	5,500	Seed	Indo Malay	P	*Sesamum indicum*
						D	*S. indicum*
Extensive experiment							
Barley	Poaceae	C_3 cereal	12,000	Seed	Palearctic	P	*Hordeum vulgare* ssp. *spontaneum*
						D	*H. vulgare* ssp. *vulgare*

Chili pepper	Solanaceae	Forb	10,000	Fruit	Neotropic	P	*Capsicum baccatum*
						D	*C. baccatum*
Flax	Linaceae	Forb	11,200	Seed	Palearctic	P	*Linum usitatissimum*
						D	*L. usitatissimum*
Lentil	Fabaceae	Legume	12,000	Seed	Palearctic	P	*Lens culinaris* ssp. *orientalis*
						D	*L. culinaris* ssp. *culinaris*
Sorghum	Poaceae	C_4 cereal	10,000	Seed	Afrotropic	P	*Sorghum arundinaceum*
						D	*S. bicolor*
Vetch	Fabaceae	Legume	9,950	Seed	Palearctic	P	*Lathyrus cicera*
						D	*L. sativus*
White clover	Fabaceae	Legume	1,650	Leaf	Palearctic	P	*Trifolium repens*
						D	*T. repens*

Experimental procedures and data compilation

The three experiments were carried out in the Cultive glasshouse at the Universidad Rey Juan Carlos (Móstoles, Spain) in spring 2018, 2019 and 2020. The advantages of glasshouse experiments are that they allow control and replication of growth conditions and ensure that all species experience the same conditions so that appropriate comparisons can be made. The specifics of each experiment are described in the chapters, but in all of them the plants were grown to maturity from seeds of germplasm banks under high availability of water, nutrients and light, and placed on two adjacent benches with a randomised block design. The selection of plant traits was based on those that allowed inferences about plant size responses to early selection, initial domestication, and further improvement. In the *intensive* and *extensive experiments*, these traits included: Seed mass, RGR and its components, duration of vegetative traits, plant biomass and size-related traits (height, canopy, number of leaves and branches, and basal stem diameter), leaf area, biomass allocation to leaves, stems, roots, and reproduction, and were taken throughout the entire plant ontogeny. In the *ecophysiological experiment*, these traits comprised leaf-level gas exchange, leaf morphology, biochemistry, and traits related to water use, and were measured on three consecutive days before flowering (Fig. 1). The protocols for measuring the selected phenotypic traits were in line with trait measurement protocol handbooks (Pérez-Harguindeguy *et al.*, 2013).

Fig. 1. Pictures showing various steps during experimental measurements (from top left to bottom right): Seeds of different accessions before weighing, measuring size-related traits, dividing the plants into their fractions, scanning the leaves to obtain leaf area, measuring gas exchange at leaf-level.

To complement data from the experiments, we also extracted ecophysiological trait data from global databases such as the TRY plant trait database (www.try-db.org) (Kattge *et al.*, 2011), the Botanical Information and Ecology Network (BIEN) database (https://bien.nceas.ucsb.edu/bien/) (Maitner *et al.*, 2018), the AusTraits database (www.austraits.org) (Falster *et al.*, 2021), the China Plant Trait Database (Wang *et al.*, 2018) and the LEDA database (www.leda-traitbase.org) (Kleyer *et al.*, 2008). The primary criterion for data compilation was to choose herbaceous species with an annual life history (for direct comparison with the annual domesticated plants and wild progenitors included in the experiments) rather than biennial or perennial species. Information on growth form and life history was extracted from the on-line database Plants of the World Online (POWO; www.plantsoftheworldonline.org). A secondary criterion was the selection of studies on ecophysiological traits of plants grown outdoors or indoors, with experiments including only control treatments (*i.e.* without light, water,

nutrient, grazing, and competition stress) and plants growing under atmospheric [CO_2]. These data enabled the inclusion of a total of 1,050 species that were never domesticated, 67 other agricultural species and 48 other crop's wild progenitors.

Statistical approach

To analyse the data from the above experiments, we first used non-linear allometric growth modelling to calculate RGR (Paine *et al.*, 2012). We fitted logistic functions to the increase in mass of each monitored plant over the vegetative growth period. Growth modelling allowed us to generate estimates of the minimum and maximum asymptotes (*i.e.* initial and final sizes), the slope at the inflection point (*i.e.* maximum growth rate), and the duration of vegetative growth. By using these curve parameters, we were able to standardise the RGR metric at a common reference size and age, which allowed us to make more accurate comparisons.

Inter-specific experiments, such as those conducted in this thesis, are a powerful tool in the search for general patterns (van Kleunen *et al.*, 2014), but the data may have phylogenetic structure that needs to be treated appropriately in statistical analyses. Therefore, the statistical methods used in this thesis controlled for variability among the different species included in the experiments. The most used were linear mixed-effects (LMM) models, where species variability was included in the random structure of the models. We also used phylogenetic generalised least squares (PGLS) models, in which the structure of phylogenetic relationships among species was incorporated in the residuals of the models.

To test multivariate hypotheses linking morpho-, physio- and phenological traits to plant size and crop yield, we used path analyses based on previous knowledge (*i.e.* confirmatory multi-level path analyses *sensu* (Shipley, 2000)). In this framework, the computation of direct and indirect effects using standardised path coefficients (Shipley, 2009) allowed us to weight the relative contribution of seed mass and growth dynamics in driving variations in mature plant size. In addition, this allowed us to assess the effects of evolution under cultivation on trait relationships and the consequences of variation in plant size on crop yields. Finally, we also used a multivariate approach to delineate the spaces of possible phenotypic combinations in wild and domesticated species. These phenotypic spaces were quantified using the hypervolume method (Blonder *et al.*, 2014). With this method, we were able to calculate the trait spaces of two sets of species (domesticated and wild species) and quantify the overlap between them.

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LIST OF MANUSCRIPTS

Chapter 1 Gómez-Fernández A, Aranda I & Milla R. Early human selection of crops' W progenitors explains the acquisitive physiology of modern cultivars. Submitted to *Nature Plants*

Chapter 2 Gómez-Fernández A, Osborne CP, Rees M, Palomino J, Ingala C, Gómez G & Milla R. (2022). Disparities among crop species in the evolution of growth rates: the role of distinct origins and domestication histories. *New Phytologist*, 233(2), 995–1010.

Chapter 3 Gómez-Fernández A & Milla R. (2022). How seeds and growth dynamics influence plant size and yield: Integrating trait relationships into ontogeny. *Journal of Ecology*, 110(11), 2684–2700.

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CHAPTER 1

Early human selection of crops' wild progenitors explains the acquisitive physiology of modern cultivars

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ABSTRACT

Crops have resource-acquisitive leaf traits, which is usually attributed to the process of domestication. However, early choices of wild plants amenable for domestication may also have played a key role in the evolution of crops' physiological traits. We compiled data on 1,034 annual herbs to place the ecophysiological traits of 69 crops' wild progenitors in the context of global botanical variation, and conducted a common-garden experiment to measure the effects of domestication on crop ecophysiology. Our study found that crops' wild progenitors already had high leaf nitrogen, photosynthesis, conductance, transpiration, and soft leaves. After domestication, ecophysiological traits varied little and in idiosyncratic ways. Crops did not surpass the trait boundaries of wild species. Overall, the resource-acquisitive strategy of crops is largely due to the inheritance from their wild progenitors rather than to further breeding improvements. Our study concurs with recent literature highlighting constraints of crop breeding for faster ecophysiological traits.

INTRODUCTION

Introduction

Modern civilisation relies on a small number of the world's *ca*. 354,000 flowering plants for its nourishment (Milla & Osborne, 2021; Qian *et al.*, 2022). Food crops evolved under cultivation from their respective wild progenitors over the last millennia (Gepts, 2001). During this process, crops tended to converge in some traits, such as large seeds with low dormancy and dispersal ability, high plant vigour and yield potential, and synchronous phenologies (Meyer & Purugganan, 2013). However, plant growth rates and other physiological traits evolved inconsistently after domestication (Evans, 1993; Gómez-Fernández *et al.*, 2022). This is puzzling, as cultivated plants typically exhibit faster growth and carbon fixation rates than wild species that were never domesticated (Nadal & Flexas, 2018; Huang *et al.*, 2022). An alternative hypothesis is that the wild progenitors of crops were physiologically distinct. Indeed, crop domestication may have already started with distinctive wild species, as proto-farmers may have consciously or unconsciously selected for cultivation wild species with particular traits (de Wet & Harlan, 1975; Cunniff *et al.*, 2014; Preece *et al.*, 2015; Spengler, 2022). However, the relative importance of 'early human selection' *vs*. 'evolution under cultivation' to explain the fast physiological rates of crops is largely unknown.

Ecophysiological traits (*i.e.* traits that influence resource use and acquisition) are key determinants of plant growth and performance and play an important role in environmental adaptation (Lambers & Oliveira, 2007). The ecophysiological traits of crops are a non-random representation of those of wild plants. For example, agricultural species tend to have higher net photosynthesis, higher stomatal and mesophyll conductances, more leaf nitrogen, and softer leaves than wild herbs (Gago *et al.*, 2014; Milla *et al.*, 2015, 2018a; Nadal & Flexas, 2018; Huang *et al.*, 2022). Other attributes related to the acquisition of resources in the soil, such as root tissue density, specific root length or root mass fraction, also differ between crops and non-crop species (Martín-Robles *et al.*, 2018). This suggests that the ability to thrive successfully under productive and fertile conditions is a common characteristic of crops (Milla *et al.*, 2018a). Despite the lack of detailed empirical evidence, the acquisitive strategy of crops has typically been attributed to selection forces operating under cultivation (Tribouillois *et al.*, 2015).

Before the advent of agriculture, hunter-gatherers harvested and used a wide array of wild food plants, but only a few of these wild foods were domesticated and made it to current-day agricultural systems (Kislev *et al.*, 2004; Weiss *et al.*, 2006). This subset of wild foods are the wild progenitors of modern crops. Whether crops' wild progenitors share a number of common traits that can differentiate them from other wild species has recently been a matter of study. For example, wild progenitors of barley, einkorn and emmer wheat have larger seedlings, faster germination and greater seed mass, growth rate, height, and yield than other wild grasses common in the Fertile Crescent (Cunniff *et al.*, 2014). In addition, seeds of cereal and legume crops' wild progenitors are larger than those of other wild species (Blumler, 1998; Preece *et al.*, 2015; Wood & Lenné, 2018). The fine roots of crops´ wild progenitors are also noticeably acquisitive compared to other wild herbs, suggesting that the roots of crops´ progenitors were already preadapted to cultivation before domestication (Martín-Robles *et al.*, 2018). Although there are hints that the choices of early farmers could have a major impact on the phenotypic profile of modern crops, a comprehensive screening comparing the ecophysiology of crops' wild progenitors with global botanical diversity is currently lacking.

In addition to early selection, the acquisitive strategy of crops could also be explained by later evolution under cultivation. Initial domestication and subsequent plant breeding have resulted in crop varieties that are phenotypically different from their wild progenitors due to several selection forces (Meyer & Purugganan, 2013). First, agricultural environments are resource-rich habitats (high availability of nutrients, light and water) that typically select for acquisitive, fast-growing plants (Milla *et al.*, 2015; Roucou *et al.*, 2017; Martin & Isaac, 2018). Second, artificial selection and modern breeding programmes have promoted high-yielding and less stress-tolerant plants, which may have led to indirect changes in correlated traits such as those related to allocation and physiological response (Hay & Porter, 2006; Preece *et al.*, 2017b). However, the effects of domestication on ecophysiological traits appear to be inconsistent or variable among crops (Evans, 1993). For example, photosynthetic rates decreased with domestication in wheat and bean (Evans & Dunstone, 1970; González *et al.*, 1995), but increased in cassava and cotton (Pujol *et al.*, 2008; Lei *et al.*, 2022), while stayed steady in rice (Giuliani *et al.*, 2013; Xiong *et al.*, 2015). Even when comparisons are performed across several crop species grown simultaneously under the same conditions, the effects of domestication on ecophysiological traits tend to vary within and among crops

(Yarkhunova *et al.*, 2016; Matesanz & Milla, 2018). Therefore, the evolution of ecophysiological traits under cultivation remains to be investigated across a wider range of crops and accessions, and a distinction needs to be made between the effects of initial domestication and of modern plant breeding.

Here, we addressed the question of which of the two processes –early human selection and/or evolution under cultivation– has led to crops having a more acquisitive ecophysiology than wild species. Both processes may have pushed crops out of the phenotypic boundaries defined by the global pool of wild species (Milla *et al.*, 2015). Therefore, we also wondered whether the acquisitive strategy of crops is so distinct as to push them outside the boundaries of the ecophysiological trait spectra of wild species (Fig. 1). To carry out the research, we first compiled a dataset (hereafter referred to as the *global dataset*) of five leaf ecophysiological traits related to carbon-water economics: net photosynthetic rate per unit area (A_{area}), stomatal conductance to water vapour (g_{wv}), mass-based foliar nitrogen concentration ($[N_{mass}]$), specific leaf area (SLA), and ^{13}C isotopic composition ($\delta^{13}C$). Using phylogenetically informed analyses, we compared the ecophysiological traits of crops' progenitors with those of other wild annual herbs. Second, we set-up a glasshouse experiment with 11 annual herbaceous crops, including progenitor, landrace and improved accessions of each crop, and measured the same ecophysiological traits that were considered in the *global dataset* (hereafter, the *experimental dataset*). By comparing wild progenitors with landraces, and landraces with improved cultivars under common-garden conditions, we addressed the effects of domestication and modern breeding, respectively. Finally, we computed the phenotypic spaces of crops and wild species, based on their ecophysiological traits, and measured their size, uniqueness and degree of overlap. Specifically, we asked: i) Do the ecophysiological traits of crops' progenitors tend to exhibit a more acquisitive strategy than other wild herbs?; ii) How have domestication and modern plant breeding impacted crop ecophysiology?; and iii) Do the ecophysiological traits of domesticated plants extend beyond the global trait variation observed in wild species?

MATERIAL AND METHODS

Data compilation

We compiled a *global dataset* of 1,147 annual herbaceous species with ecophysiological data from diverse databases, published articles and unpublished data. The ecophysiological traits considered in this compilation were net photosynthetic rate per unit area (A_{area}; μmol CO_2 m^{-2} s^{-1}), stomatal conductance to water vapour (g_{wv}; mol H_2O m^{-2} s^{-1}), mass-based foliar nitrogen concentration ([N_{mass}]; %), specific leaf area (SLA; cm^2/g), and ^{13}C isotopic composition ($\delta^{13}C$; ‰). The vast majority of data were compiled from the TRY plant trait database (Kattge *et al.*, 2011) (www.try-db.org), the Botanical Information and Ecology Network (BIEN) database (Maitner *et al.*, 2018) (https://bien.nceas.ucsb.edu/bien/), the AusTraits database (Falster *et al.*, 2021) (www.austraits.org), the China Plant Trait Database (Wang *et al.*, 2018), and the LEDA database (Kleyer *et al.*, 2008) (www.leda-traitbase.org). The dataset was supplemented by published data not included in the former databases (Hanba *et al.*, 2010; Delgado-Baquerizo *et al.*, 2016; Milla *et al.*, 2018a; Nadal & Flexas, 2018; Matesanz & Milla, 2018; Marques *et al.*, 2020; Preece *et al.*, 2021; Simpson *et al.*, 2021; Neto-Bradley *et al.*, 2021; Jiménez-Leyva *et al.*, 2022; Huang *et al.*, 2022; Gómez-Fernández *et al.*, 2022) and from data of our own experiment (see section 'Glasshouse experiment' below).

Data were filtered to include only herbs and grasses, but not bamboos, carnivores, climbers, epiphytes, geophytes, helophytes, lianas, parasites, shrubs, succulents, trees, and vines, based on growth form information from the databases or from the Plants of the World Online (POWO) database (www.plantsoftheworldonline.org). The search was oriented to papers on ecophysiological traits of plants grown in the field or under controlled environmental conditions. In case of experimental studies, we only considered control treatments (*i.e.* without light, water, nutrient, grazing, or competition stress) and plants growing under atmospheric [CO_2]. We also excluded non-food crops and their direct wild progenitors (*i.e.* extant wild taxa most closely related to the crop's ancestor), based on the Crop Origins database (Milla, 2020). We focused on annual plants because most major food crops are annuals, and comparisons with wild species of other life cycles might be misleading. We recorded information on photosynthetic pathway (C_3 *vs.* C_4), as it determines very distinct patterns of ecophysiological traits (Pearcy & Ehleringer, 1984). The species compiled for each ecophysiological trait and associated reference/database

can be found in Table S5. Plant taxonomy was standardised according to the Leipzig Catalogue of Vascular Plants (LCVP) as the most up-to-date and comprehensive reference dataset currently available for vascular plants, using the 'LCVP' and 'lcvplants' R packages (Freiberg *et al.*, 2020).

Glasshouse experiment

Plant material

We built the *experimental dataset* by setting up a glasshouse experiment and collecting the same ecophysiological traits as in the *global dataset*, but over the domestication history of 11 annual herbaceous crops. The studied crops belong to diverse families: Amaranthaceae, Asteraceae, Boraginaceae, Brassicaceae, Fabaceae, Malvaceae, Pedaliaceae, Poaceae and Solanaceae, and have different photosynthetic pathways: C_3 and C_4 (Table S6). For each crop, we distinguished three domestication statuses: wild progenitors, landraces, and improved cultivars. Landraces are domesticated genotypes that have not been intensively bred in the last centuries, and improved cultivars are the last improved domesticated plants resulting from intensive breeding programmes since the decade of the 1950s, with the onset of the Green Revolution. For each domestication status and crop, we obtained seeds from two accessions, for a total of 66 accessions (see Table S6 for accession identifiers and seed donors).

In May 2020, ca. 30 seeds of each accession were sown on cell-pack flats. After germination, four seedlings per accession were randomly selected and transplanted to single-plant pots (3.6 L; 15 × 15 × 20 cm). Pot size was chosen to minimize growth restriction for the largest species (Poorter *et al.*, 2012a). All pots were filled with washed sand and supplied with 18 g of a slow-release fertiliser (5 g L^{-1}; Basacote Plus 6 M, Compo, Barcelona, Spain). The amount of fertiliser was set according to the manufacturer's recommended dose for high nutrient availability conditions. Plants were grown indoors in the CULTIVE lab glasshouse at Universidad Rey Juan Carlos (Móstoles, Spain) from May to July 2020. Plants were irrigated to field capacity daily and grown with ambient light at mean photosynthetically active radiation (PAR) of 900 ± 200 μmol m^{-2} s^{-1} during light hours, with day/night temperatures of 28/20 ± 4 °C, and a relative humidity of 56 ± 15%. The sample size of the experiment was 264 plants (66 accessions × 4 replicates).

Trait measurements

We took leaf-level measurements of gas exchange, morphology and chemistry. First, gas exchange was measured between 10 am and 1 pm on three consecutive sunny days in June, before the plants reached the reproductive stage. Eight randomly chosen plants per crop were measured on each day, following a fixed order by species (cabbage, amaranth, sesame, borage, tomato, faba bean, peanut, oat, millet, lettuce, and okra). For each plant, A_{area} (μmol CO_2 m^{-2} s^{-1}), g_{wv} (mol H_2O m^{-2} s^{-1}), intrinsic water-use efficiency (iWUE = A_{area}/g_{wv}, μmol CO_2 mol^{-1} H_2O), electron transport rate (ETR, μmol electrons m^{-2} s^{-1}), and photochemical efficiency (Fv'/Fm') were measured using an infrared gas analyser (LI-6400; Li-Cor Inc., Lincoln, NE, USA). We used the youngest, unshaded, fully expanded leaf from each individual. Measurements were made under standardized conditions: ambient [CO_2] (C_a = 400 ppm), saturating irradiance (PAR = 1000 μmol m^{-2} s^{-1}), and a flow gas of 500 μmol s^{-1}. The relative humidity (RH) and air temperature (T) inside the chamber were kept constant and close to ambient conditions (RH ~ 55%; T~25°C). Measurements were recorded only when the stability criteria were met (LI-6400 User's Manual, Li-COR Inc.). If the leaf did not completely cover the chamber (*e.g.* for oats), leaf fragments were scanned and the area calculated using Photoshop software (CS6; Adobe Systems, Inc., San Jose, CA, USA) to recalculate gas exchange values.

Second, we measured SLA (cm^2/g) as a leaf morphological trait. Two discs (5 mm diameter) of leaf laminae without major veins were taken from the same leaf used for the gas exchange measurements, using a paper punch. All discs were oven-dried at 60 °C for three days and then weighed on a microbalance (accuracy 1 μg; Mettler Toledo, Columbus, OH, USA) to obtain leaf discs dry mass. SLA was calculated as the ratio of leaf discs area to leaf discs dry mass. Net photosynthetic rate per unit mass (A_{mass}; μmol CO_2 g^{-1} s^{-1}) was then calculated as the product of SLA and A_{area}.

Third, we collected data on leaf chemistry. For each individual plant, the two leaf discs were sealed in a tin capsule. Total leaf C and N content (μg) and the ratio of stable isotopes ^{13}C:^{12}C ($\delta^{13}C$, ‰) and ^{15}N:^{14}N ($\delta^{15}N$, ‰) per sample were measured using an elemental analyser coupled to a stable isotope mass spectrometer (IRMS; Stable Isotope Facility, University of California, Davis, USA). To determine leaf C content per unit mass (C_{mass} μg/μg) and leaf N content per unit mass (N_{mass}, μg/μg), their total content was divided by the leaf discs dry mass. Leaf C content per unit area (C_{area}) and leaf N-content

per unit area (N_{area}) were calculated as the product of SLA and C_{mass} or N_{mass}, respectively. We also computed leaf CN stoichiometry (CN, μg/μg) as the ratio of C_{mass} to N_{mass}, and mass-based leaf N concentration ([N_{mass}], %) by multiplying N_{mass} by 100. Finally, photosynthetic N use efficiency (PNUE, μmol CO_2 mol^{-1} N s^{-1}) was calculated by dividing A_{mass} by N_{mass}.

Data analyses

Question 1

To assess whether the ecophysiological traits of crops' wild progenitors differ from those of other wild herbaceous species, we performed phylogenetic generalized least squares (PGLS) models, using the *global dataset*. PGLSs include phylogenetic correlation structure in model residuals to account for species' non-independence due to phylogenetic relatedness (Symonds & Blomberg, 2014). Ecophysiological traits were included as response variables and plant type (categorical variable: crop's wild progenitor *vs*. other wild annual herb) and photosynthetic pathway (categorical variable: C_3 *vs*. C_4) as predictors. To perform the PGLSs, we first built a phylogenetic tree for the 1,147 annual herbaceous species in our *global dataset*. This phylogenetic tree was derived from the most updated and expanded mega-tree of angiosperms (GBOTB.extended.LCVP.tre (Jin & Qian, 2022)). Of the 1,147 species in our *global dataset*, 808 (70 %) were included in the mega-tree. The remaining 339 were added to our tree as polytomies at the middle point of the corresponding genus branch, using the *phylo.maker* function with scenario three in the 'V.PhyloMaker2' R package (Jin & Qian, 2022), as recommended by (Qian & Jin, 2021). To account for phylogenetic uncertainty, all analyses were performed on 1000 randomly resolved trees by using the *fix.poly* function of the 'RRphylo' R package (Castiglione *et al.*, 2018). PGLSs were implemented using the *gls* function with corPagel phylogenetic correlation structure in the 'nlme' R package (Pinheiro *et al.*, 2021) and the significance of predictors was estimated using the *anova* function with sequential (type II) sums of squares in the same R package.

Question 2

The *experimental dataset* was used to assess the effects of domestication and subsequent improvement on ecophysiological traits. We performed linear mixed-effect models (LMMs), using the *lme* function in the 'nlme' R package (Pinheiro *et al.*, 2021). Models included each ecophysiological trait as a response variable and domestication status (wild,

landrace, improved) as fixed effects. Accession nested within crop species was considered as random factor. Log_{10}-transformations were used when appropriate to meet assumptions of the models. In the presence of heteroscedasticity (verified with the Levene's test), the variance structure of the data was modelled using the weights option (VarInt comand) within the *lme* function. Significance of the fixed factors of the models was estimated by using the *anova.lme* function with sequential (type II) sums of squares in the 'nlme' R package (Pinheiro *et al.*, 2021). The amount of variance explained by the models was evaluated using the *r.squaredGLMM* function from the 'MuMIn' R package (Barton, 2020). Pairwise comparisons among domestication statuses and species were performed using the *pairwise_t_test* function in the 'rstatix' R package (Kassambara, 2021) with false discovery rate control.

Question 3

To measure the size, uniqueness and overlap of the phenotypic space of crops *vs*. that of wild species, we used the hypervolume approach of Blonder *et al*. (Blonder *et al.*, 2014, 2018). This approach quantifies the n-dimensional phenotypic space using a set of observations and assuming kernel density estimation, and estimates shared and unshared trait combinations between two or more groups. Compared to previous mathematical approaches, it is not sensitive to outliers, can detect gaps (or holes) and allows resampling to correct for sample size effects (Blonder, 2016).

First, we built a two-dimensional space for each bivariate trait combination and each plant type (crop *vs*. wild), using the *global dataset*. In the wild-type subset, we excluded crops' wild progenitors, as they are part of the primary gene pool of crops and in most cases belong to the same species. The number of dimensions was set to n = 2 in order to have enough number of data points for computing the hypervolumes (*i.e.* roughly <10 times the number of dimensions (Blonder *et al.*, 2014)) and to increase interpretability by displaying specific ecophysiological traits in the hypervolume axes. Traits were log_{10}-transformed and scaled (mean = 0 and SD = 1). Since all values of $\delta^{13}C$ were negative, we log_{10}-transformed and scaled its absolute values. For each trait combination, a principal component analysis (PCA) was performed on the wild- and crop-type subsets together, as hypervolume calculations can be sensitive to collinear variables (Blonder *et al.*, 2014). Separate hypervolumes were then calculated from the two PCA axes corresponding to each subset. There were less crops than wild species and the

proportion of C_4 species was higher in the wild-type subsets. To account for these differences, the number of wild species and the proportion of C_4 wild species was matched to that of crops to thus make the size of phenotypic spaces comparable (see 'species sample' and 'percent of C_4' columns in Table S4). Therefore, the phenotypic spaces of wilds were generated from 1000 randomly sampled subsets by sampling with replacement the same number of points and the same proportion of C_4 species in the wild-type than in the crop-type subset (Lamanna *et al.*, 2014). PCAs were performed using the *PCA* function of 'FactoMineR' R package (Lê *et al.*, 2008) and phenotypic spaces were calculated based on Gaussian kernel density estimation using the *hypervolume_gaussian* function with default settings (Silverman bandwidth estimator and 95% probability threshold) in the 'hypervolume' R package (Blonder *et al.*, 2022). Finally, we calculated the mean size and standard deviation of all phenotypic spaces.

Second, we calculated the phenotypic overlap between the two plant types. We defined overlap as the ratio of the size of the intersection over union (Jaccard index: $(A \cap B)/(A \cup B)$). Trait space overlap represents the similarity of the wild- and crop-type phenotypic spaces, with values ranging from 0 (species are completely dissimilar) to 1 (species are completely similar). For each trait pair, we computed the intersection, union and unique components of all pairwise phenotypic space combinations using the *hypervolume_set* function in the 'hypervolume' R package (Blonder *et al.*, 2022). To ensure that our results were not biased by the species selected in the random sample, we repeated each pairwise analysis on the 1000 random wild subsets. For each pairwise combination, we then calculated the Jaccard index and the unique fraction of each plant type, and reported the mean and standard deviation for each trait pair. Finally, to test the significance of statistics, we built up hypervolumes based on null expectations. Specifically, we generated a 100-sized randomized distribution for the Jaccard index and unique fractions under the null hypothesis that the wild- and crop-type phenotypic spaces were drawn from both plant types. We then calculated the *P*-value for each observed statistic with respect to the generated null distribution using the *hypervolume_overlap_test* function in the 'hypervolume' R package (Blonder *et al.*, 2022), and reported the median *P*-value.

RESULTS

Our *global dataset* included ecophysiological trait data on 1,147 annual herbs, including domesticates, crops' wild progenitors and wild species (Table S1). The set of crops retrieved in this compilation accounts for the crop species grown in 75% of global croplands (http://faostat.fao.org, 2021 data). Each leaf trait varied by up to two orders of magnitude and was dependent on photosynthetic pathway and phylogenetic history (Fig. 2, Table S2 and Fig. S1). On average, C_4 species had lower g_{wv}, lower [N_{mass}] and more $\delta^{13}C$ than C_3 species (Fig. 2, Table S2a and Fig. S1). The pattern of trait correlations also differed by photosynthetic pathway (Fig. S2). Traits were phylogenetically non-independent, as indicated by moderate or high phylogenetic signals (Table S2).

Crops' wild progenitors differed from other wild annual herbs for all five ecophysiological traits studied, irrespective of their phylogenetic context (Fig. 2, Table S2). The wild progenitors of crops had higher A_{area}, g_{wv}, [N_{mass}], and SLA and lower $\delta^{13}C$ in comparison with the data from other annual herbs (Fig. 2, Table S2a). The same pattern was observed when domesticates were compared to wild herbs (Fig. S1). When field studies were excluded to control for confounding environmental factors, crops' progenitors also exhibited more acquisitive ecophysiological traits than other wild species (except for [N_{mass}]; Table S2b). The higher acquisitive profile of crops' wild progenitors was more prominent in some botanical orders (*e.g.* Poales) than in others (*e.g.* Fabales, Caryophyllales; Fig. 2).

The range of ecophysiological traits in our *experimental dataset* encompassed a small-to-average portion of the variation in these plant traits found in the *global dataset* (15% for A_{area}, 28% for g_{wv}, 3% for [N_{mass}], 20% for SLA, and 55% for $\delta^{13}C$). The effects of domestication were small in magnitude and diverse among crops and accessions within crops (Fig. 3 and Fig. S3). Most crops showed no domestication effects; only lettuce showed a modest decrease in A_{area} and g_{wv}, while tomato a slight increase in A_{area} and SLA (Fig. S3). Domestication tended to decrease [N_{mass}] and increase $\delta^{13}C$ (Table S3), but with a small effect size, so that none of the specific landraces differed from their wild progenitors when compared pairwise by species (Fig. S3). We found no effect of modern breeding (*i.e.* no differences between landraces and modern cultivars) for any of the ecophysiological traits (Fig. 3, Table S3 and Fig. S3).

Crops took almost half of the phenotypic space of wild species, with Jaccard indices ranging from 38 to 50 % (Fig. 4 and Table S4). However, trait combinations differed between plant types, with crops occupying the acquisitive end of the wild-type phenotypic spaces (Fig. 4 and Table S4). Crops had smaller phenotypic spaces in seven of the ten trait combinations that included A_{area} and g_{wv} (Fig. 4 and Table S4). The unique fractions of crop trait spaces were small and not significantly different from null expectations, except for [N_{mass}] and $\delta^{13}C$ (Table S4). C_4 crops showed the most unique trait combinations, with distinct [N_{mass}] and $\delta^{13}C$ values as compared to the phenotypic space of wild herbs (Fig. S4).

DISCUSSION

The comparative analysis of 1,104 herbaceous species showed that the direct wild progenitors of major food crops have a more acquisitive ecophysiology than other wild annual herbs that never became domesticated. On average, crops' wild progenitors had higher photosynthetic rates, stomatal conductances, leaf nitrogen, softer leaves, and lower water use efficiency (*i.e.* higher $\delta^{13}C$) than other wild herbs. Further evolution under cultivation did not consistently change ecophysiological traits. Domesticated plants have maintained the variation of ecophysiological traits within the range already set by their wild progenitors. Accordingly, the phenotypes of domesticates laid within the trait space occupied by wild annuals, but crops tended to cluster at the acquisitive end of the spectra of variation. Overall, our findings highlight the importance of early human selection over further breeding improvements for the prevalence of acquisitive strategies in modern cultivars. This has important implications both for our understanding of the origins of agriculture and for gaining insights into the evolutionary potential and constraints of crop ecophysiology.

We found that crops' wild progenitors tend to have more acquisitive ecophysiological traits compared to other wild species. Acquisitive strategies had previously been described as a distinctive characteristic of crops *vs.* wild species (Tribouillois *et al.*, 2015; Roucou *et al.*, 2017; Milla *et al.*, 2018a; Nadal & Flexas, 2018; Huang *et al.*, 2022). However, these studies included a limited number of crop species and traits, did not distinguish between crop progenitors and other wild species, and/or

only considered growth form as a factor that could influence leaf economics. Ecophysiology also depends on life cycle, photosynthetic pathway and phylogeny, and shows high sensitivity to environmental conditions (Bazzaz, 1979; Pearcy & Ehleringer, 1984; Gago *et al.*, 2019). In contrast to other studies, our analyses were restricted exclusively to annual species, which include the progenitors of most major food crops, to account for differences in growth according to life cycle. In addition, they controlled for photosynthetic pathway and phylogeny, and distinguished between plants grown in the field and under controlled conditions. Based on more targeted comparisons and a global-scale data compilation, we found that domesticated plants do have an acquisitive physiology and are less efficient in water use, but this profile was already in their wild progenitors. The magnitude of trait differences between crop progenitors and other wild species differed across phylogenetic clades. Several explanations might account for such diversity between phylogenetic groups, including differences in growth habit, habitat preference and plant stature, which covary with physiological traits (Abbo *et al.*, 2009). Thus, in addition to the generalized acquisitive profile of crops' wild progenitors, other traits which differ between phylogenetic clades, influenced on why certain wild species were chosen by early farmers.

The acquisitive physiology of crops' wild progenitors may reflect their pre-adaptation to early anthropogenic environments. This hypothesis was first proposed by Engelbrecht (1916) (Engelbrecht, 1916), who suggested that early human selection may have favoured traits that were advantageous in the nutrient-rich habitats around human settlements (the so-called 'dump heap hypothesis' (Hawkes, 1969)). If so, crops' wild progenitors would be either ruderal or competitive plants characterised by relatively rapid growth and high resource uptake rates (Grime, 1979). In support of this hypothesis, some studies have shown that crops' progenitors grow faster and have more acquisitive traits compared to other wild species (Cunniff *et al.*, 2014; Martín-Robles *et al.*, 2018), but the results are diverse in terms of reproductive allocation and phenology, *i.e.* traits that distinguish ruderal from competitive plants (Cunniff *et al.*, 2014; Preece *et al.*, 2015, 2017a). Although our study places crops' wild progenitors on the fast end of the leaf economics spectrum (Wright *et al.*, 2004), further studies encompassing a wider range of phenotypic traits at different levels of organization would be needed to establish whether wild progenitors are predominantly ruderals or competitors. Another, non-exclusive, alternative hypothesis is that crops' progenitors are more palatable and/or nutritious than

other wild herbs. Indeed, the levels of secondary compounds, such as those related to toxicity, are lower in wild species of genera with crops' wild progenitors than in genera without them (Garibaldi *et al.*, 2021). Investment in defence often trades-off with ecophysiological traits promoting growth and yield (Zangerl *et al.*, 1997; Bekaert *et al.*, 2012), and nutritional quality is associated with higher nutrient concentrations in plant tissues (Fernandez *et al.*, 2021; Chapuis *et al.*, 2023). Therefore, by choosing more palatable or nutrient-rich plants, early farmers could have indirectly selected for plants with more acquisitive ecophysiology. Further experimental evidence looking at plant defence and nutritional quality traits is needed to test this hypothesis.

Our results showed small and generally non-consistent effects of domestication and improvement on ecophysiological traits, suggesting that evolution under cultivation has not substantially changed crop ecophysiology. The few experiments that grew sets of crops and their wild progenitors in common gardens, and measured photosynthesis and other ecophysiological traits, tended to concur with our results (Milla *et al.*, 2014; Matesanz & Milla, 2018). Variation in ecophysiological traits is often constrained by covariation with other phenotypic traits at the leaf- and whole-plant levels. For example, crops tend to be larger and have larger leaves than their wild progenitors (Milla & Matesanz, 2017). An increase in leaf size is associated with higher construction and maintenance costs per unit leaf area, at the expense of lower investment in photosynthetic machinery (Niklas *et al.*, 2007). Larger leaves and plants also require more supporting tissues such as petioles and stems, diverting resources from source tissues (Poorter *et al.*, 2012b). Moreover, photosynthetic capacity is limited by the balance between three factors: stomatal, mesophyll conductance, and photochemistry, implying a complex co-regulatory scenario (Gago *et al.*, 2019). Scaling the complexity of the three limiting factors has proven difficult and could constrain the evolution of higher photosynthetic rates in crops (Flexas & Carriquí, 2020). For example, a more even distribution of stomata between both leaf sides after domestication did not lead to an increase in photosynthesis, which may be due to a trade-off with other limiting factors (Gago *et al.*, 2019) or a saturation of effective stomatal conductance (Mott *et al.*, 1982). Further, domestication started with acquisitive species, *i.e.* crops´ wild progenitors, which might have prevented further improvements in crop ecophysiology (Milla, 2023).

Domesticated plants clustered at the acquisitive end of ecophysiological trait co-variation spaces. Thus, there is segregation in trait space between crop and wild plants for ecophysiological traits, in line with findings for other traits (Lin *et al.*, 2011b; Milla *et al.*, 2015, 2018b; Tribouillois *et al.*, 2015; Martin *et al.*, 2018). We also found differences in the size of phenotypic spaces between crops and wilds. Crops tended to have smaller ecophysiological spaces, suggesting that crops are not only highly acquisitive species, but also have less variable phenotypes than wild species. Reductions in crop phenotypic variability have also been observed in other studies (Lin *et al.*, 2011a), as well as in genetic diversity (the so-called bottleneck effect (Hyten *et al.*, 2006; Glémin & Bataillon, 2009; Purugganan & Fuller, 2009)). Even studies that have considered factors promoting evolutionary diversification of crops, such as phylogenetic origins, geographic spread and diversity in domestication purposes, have found that crops have low internal phenotypic diversity (Gómez-Fernández *et al.*, 2022). We found the same trend here after comparing the crop- and wild-phenotypic spaces at equal sample sizes, controlling the effect of species richness. We suggest that the constrained phenotypic spaces of crops and their acquisitive strategy may be a consequence of phenotypic canalization, resulting from the inheritance of their wild progenitors, which already harboured reduced phenotypic variance in their ecophysiological traits. Although intraspecific variation was not considered here, the study of trait spaces within species and the processes that shaped them should also be further explored to understand the evolutionary potential of ecophysiological traits.

Finally, the phenotypic spaces of crops did not extend beyond the ecophysiological boundaries observed in the wild plants. In other words, crops did not overcome the constraints and trade-offs that determine trait-trait correlation patterns and limit phenotypic diversity in wild species. This is consistent with previous studies suggesting that artificial selection has limited potential to shift phenotypes beyond those observed in the wild (Donovan *et al.*, 2014; Rotundo & Cipriotti, 2017; Milla *et al.*, 2018a; Garibaldi *et al.*, 2021). However, these studies focused on intraspecific variation or a limited number of traits and did not explicitly analyse trait spaces using probability density functions and weighted sample sizes. By quantifying unique fractions, our results support this general trend, but also highlight that the only crops that have explored new phenotypic regions within the leaf economics spectra of wild species are those with C_4 physiology. The events that led to the CO_2-concentrating mechanism of C_4 species

occurred relatively recently (Christin & Osborne, 2014), and this evolutionary innovation may have provided greater scope for improvements in leaf-level N and water use efficiencies.

Our findings have important ecological and agricultural implications. Placing crops' wild progenitors in the context of global botanical diversity, helps to understand why modern crops are acquisitive and fast-growing species, and provides insights into the origins of agriculture. Crops' wild progenitors are noticeably acquisitive, and during domestication and subsequent plant breeding, there has not been a further evolution of the acquisitive strategy. Moreover, our results show almost no tendency for the ecophysiological traits of domesticated plants to fall outside the range limits set by wild species. Therefore, artificial selection for acquisitive traits may be compromised by inherent trade-offs between traits at different plant organizational levels and by limiting factors of photosynthetic capacity. This paper calls for a thorough investigation of the constraints of artificial selection on ecophysiological traits to redirect future breeding efforts and ensure the productivity and stability of agriculture.

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FIGURES

Fig. 1 Conceptual framework. (a) Previous work has shown that agricultural species have a more acquisitive ecophysiological profile than wild species (Nadal & Flexas, 2018; Huang *et al.*, 2022). This observed pattern can be attributed to two processes –early human selection of crops' wild progenitors and/or further evolution under cultivation–. (b) Early selection might have led to crops' progenitors having more acquisitive ecophysiological traits compared to other wild annuals. (c) Natural and artificial selection during domestication (progenitor *vs*. landrace) and improvement (landrace *vs*. improved) might have promoted acquisitive and fast-growing crops. (d) The combined effect of both processes would reflect differences in the range of trait variation among all plant types and (e) might have caused domesticated plants to fall outside the phenotypic space of wild species. Drawings represent *Anthoxanthum odoratum* (wild herb), *Triticum dicoccoides* (crop's wild progenitor), *Triticum dicoccum* (landrace) and *Triticum durum* (improved cultivar).

Fig. 2 Early human selection. Ecophysiological traits of wild annuals compared to the wild progenitors of crops. Crops' wild progenitors (P) are shown in purple and other wild annual herbs (W) in green. Symbols indicate photosynthetic pathway: C_3 (circles) *vs*. C_4 (triangles). Points are trait means of species grouped by botanical order. Statistical differences were evaluated from phylogenetic generalized least squares (PGLS) models across 1000 randomly resolved trees (Table S2) and asterisks denote the mean *P*-value (·, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Total sample size is shown for each trait, plant type (P *vs*. W) and photosynthetic pathway. Abbreviations: A_{area}, net photosynthetic rate per unit area; g_{wv}, stomatal conductance to water vapour; [N_{mass}], leaf N concentration; SLA, specific leaf area; and $\delta^{13}C$, ^{13}C isotopic composition.

Fig. 3 Evolution under cultivation. Effects of domestication and improvement on the ecophysiological traits of crops. Wild progenitor (P; purple), landrace (L; yellow) and improved (I; coral) accessions for 11 annual herbaceous crops are plotted separately by photosynthetic pathway: C_3 *vs*. C_4. Boxplots show the median and 25^{th} and 75^{th} percentiles of the data, with whiskers extending to 1.5 times the interquartile range. Dot colours indicate accession identifier (n = 66). Differences between domestication statuses within each crop were analysed by Student's t-test and false-discovery rate correction (·,

$P < 0.1$; *, $P < 0.05$). For each ecophysiological trait, a linear mixed-effects model was run with domestication (P, L) or improvement (L, I) as a fixed effects and accession nested within crop species as random effects (significance at the bottom of each panel). Abbreviations: A_{area}, net photosynthetic rate per unit area (μmol m^{-2} s^{-1}); g_{wv}, stomatal conductance to water vapour (mmol H_2O m^{-2} s^{-1}); [N_{mass}], mass-based leaf N concentration (%); SLA, specific leaf area (cm^2 g^{-1}); and $\delta^{13}C$, ^{13}C isotopic composition (‰).

Fig. 4 Domesticates *vs*. wilds. Bivariate relationships between five ecophysiological traits, showing the phenotypic space overlap of domesticates (D; orange) and wild annual herbs (W; green). The lower left triangle of the matrix shows two-dimensional probability density distributions derived through Gaussian kernel density estimation. Traits were log_{10}-transformed and scaled. Points are species means. Symbols indicate photosynthetic pathway: C_3 (circles) *vs*. C_4 (triangles). The colour gradient indicates regions of highest (dark) to lowest (pale) occurrence probability of trait combinations with contour lines indicating 0.5 and 0.95 quantiles. The upper right portion shows comparative analyses on pairwise phenotypic spaces, where the numbers at the extremes specify the percentage of area unique to each plant type and the numbers in the middle indicate the overlapping percentage (*i.e.* Jaccard index). Significant values ($P < 0.05$) are highlighted in bold, and mean significant differences from null distributions generated from random pairwise comparisons. The diagonal displays the total sample sizes for each trait, plant type (D *vs*. W) and photosynthetic pathway. For trait abbreviations and units see legend to Fig. 3.

Fig. 1

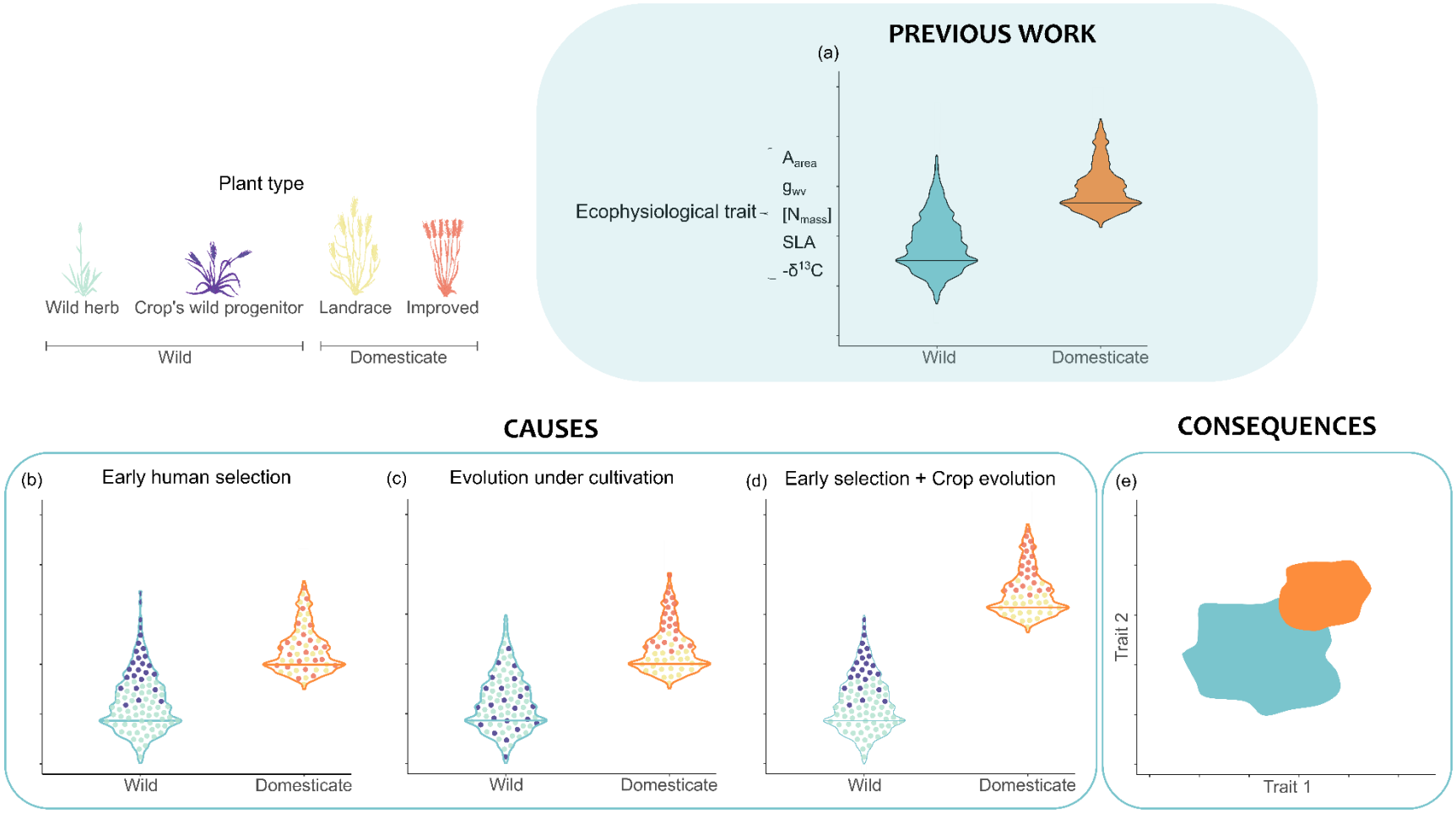

Plant type
Wild herb
Crop's wild progenitor
Landrace
Improved
Wild
Domesticate
PREVIOUS WORK
(a)
Ecophysiological trait
A_{area}
g_{wv}
$[N_{mass}]$
SLA
$-\delta^{13}C$
Wild
Domesticate
CAUSES
(b) Early human selection
Wild
Domesticate
(c) Evolution under cultivation
Wild
Domesticate
(d) Early selection + Crop evolution
Wild
Domesticate
CONSEQUENCES
(e)
Trait 2
Trait 1

Fig. 2

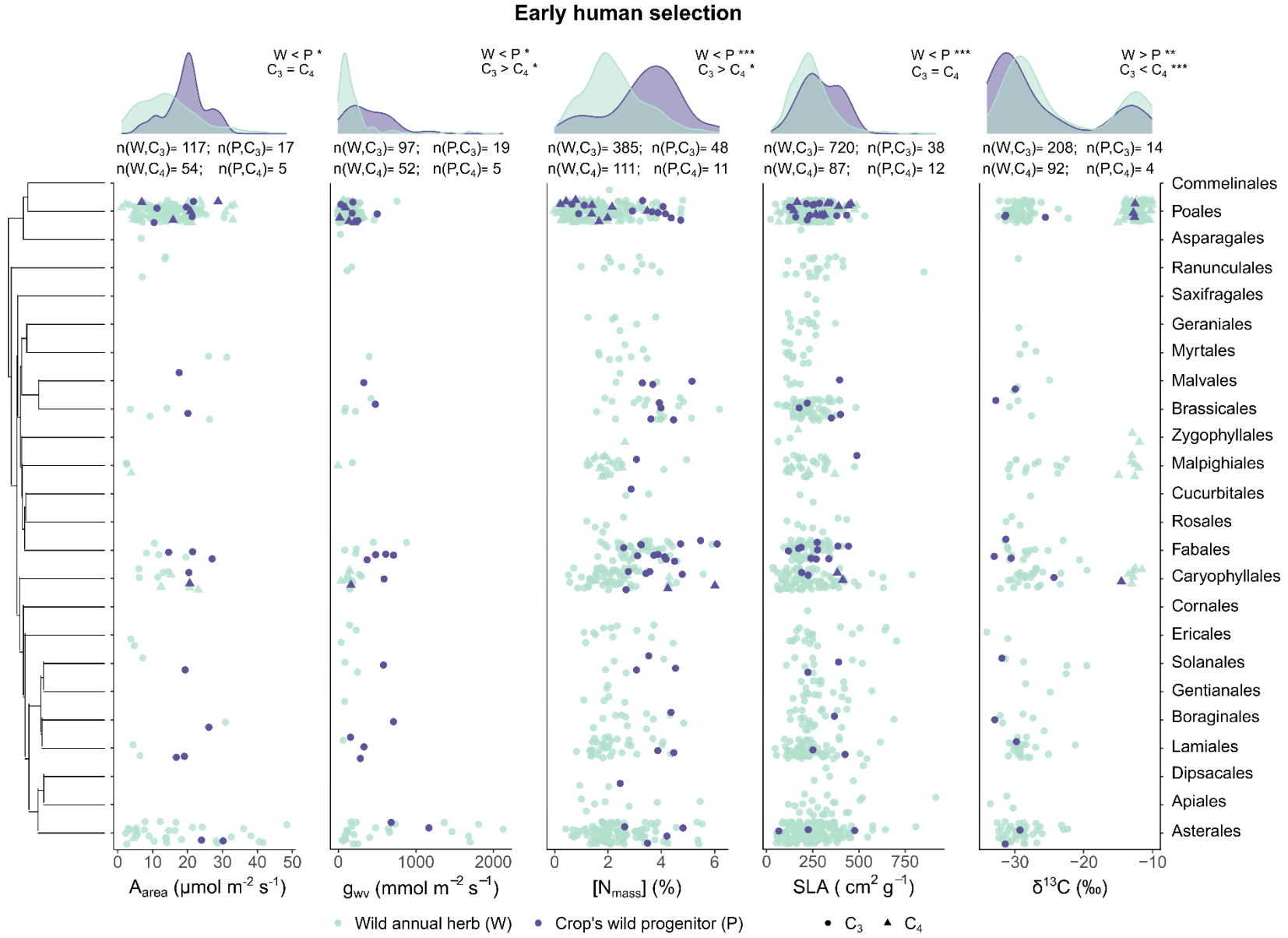

Early human selection
W < P *
C3 = C4
W < P *
C3 > C4 *
W < P ***
C3 > C4 *
W < P ***
C3 = C4
W > P **
C3 < C4 ***
n(W,C3)= 117; n(P,C3)= 17
n(W,C4)= 54; n(P,C4)= 5
n(W,C3)= 97; n(P,C3)= 19
n(W,C4)= 52; n(P,C4)= 5
n(W,C3)= 385; n(P,C3)= 48
n(W,C4)= 111; n(P,C4)= 11
n(W,C3)= 720; n(P,C3)= 38
n(W,C4)= 87; n(P,C4)= 12
n(W,C3)= 208; n(P,C3)= 14
n(W,C4)= 92; n(P,C4)= 4
Commelinales
Poales
Asparagales
Ranunculales
Saxifragales
Geraniales
Myrtales
Malvales
Brassicales
Zygophyllales
Malpighiales
Cucurbitales
Rosales
Fabales
Caryophyllales
Cornales
Ericales
Solanales
Gentianales
Boraginales
Lamiales
Dipsacales
Apiales
Asterales
0 10 20 30 40 50
Aarea (μmol m-2 s-1)
0 1000 2000
gwv (mmol m-2 s-1)
0 2 4 6
[Nmass] (%)
0 250 500 750
SLA (cm2 g-1)
−30 −20 −10
δ13C (‰)
Wild annual herb (W)
Crop's wild progenitor (P)
C3
C4

Fig. 3

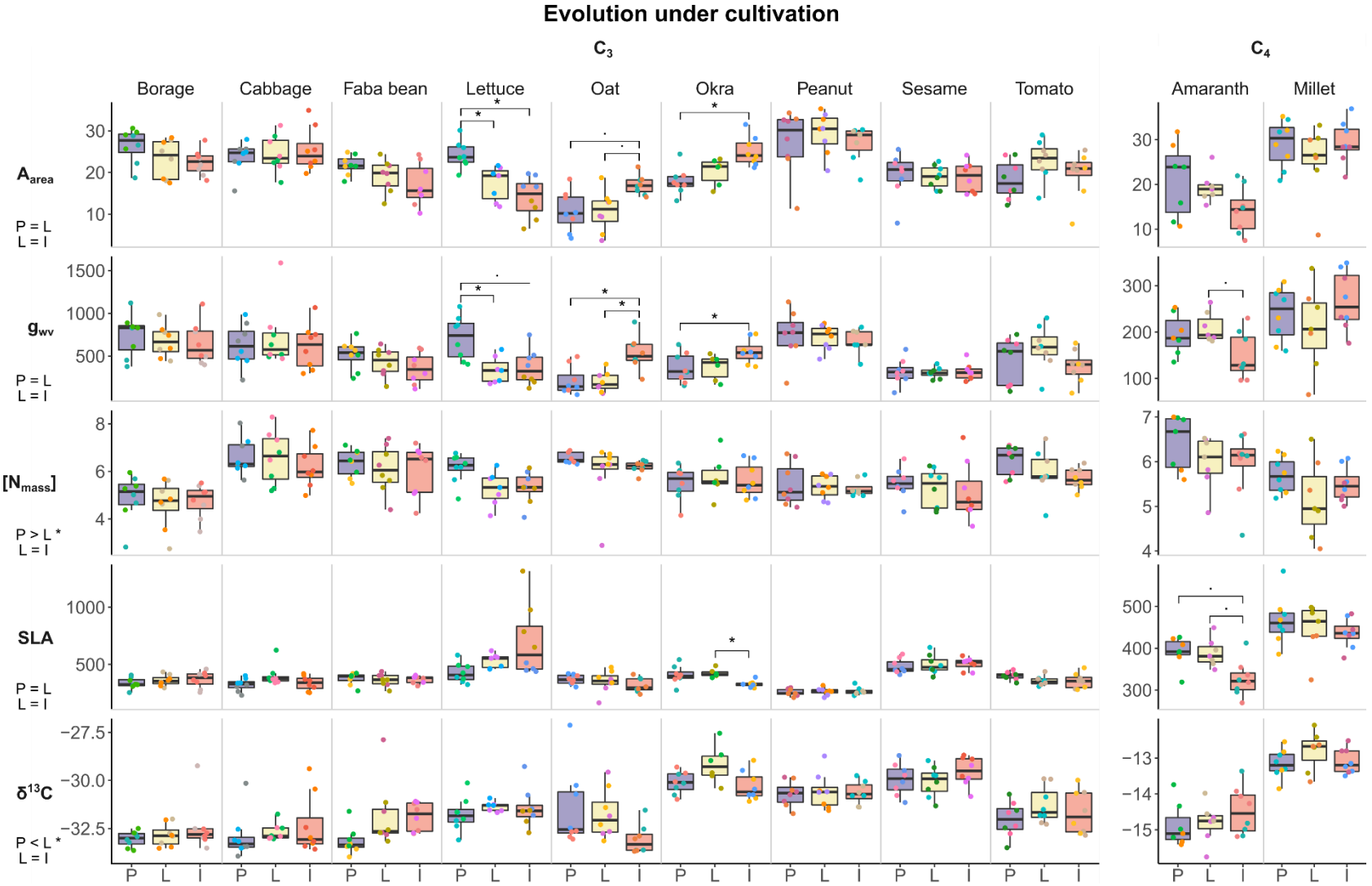
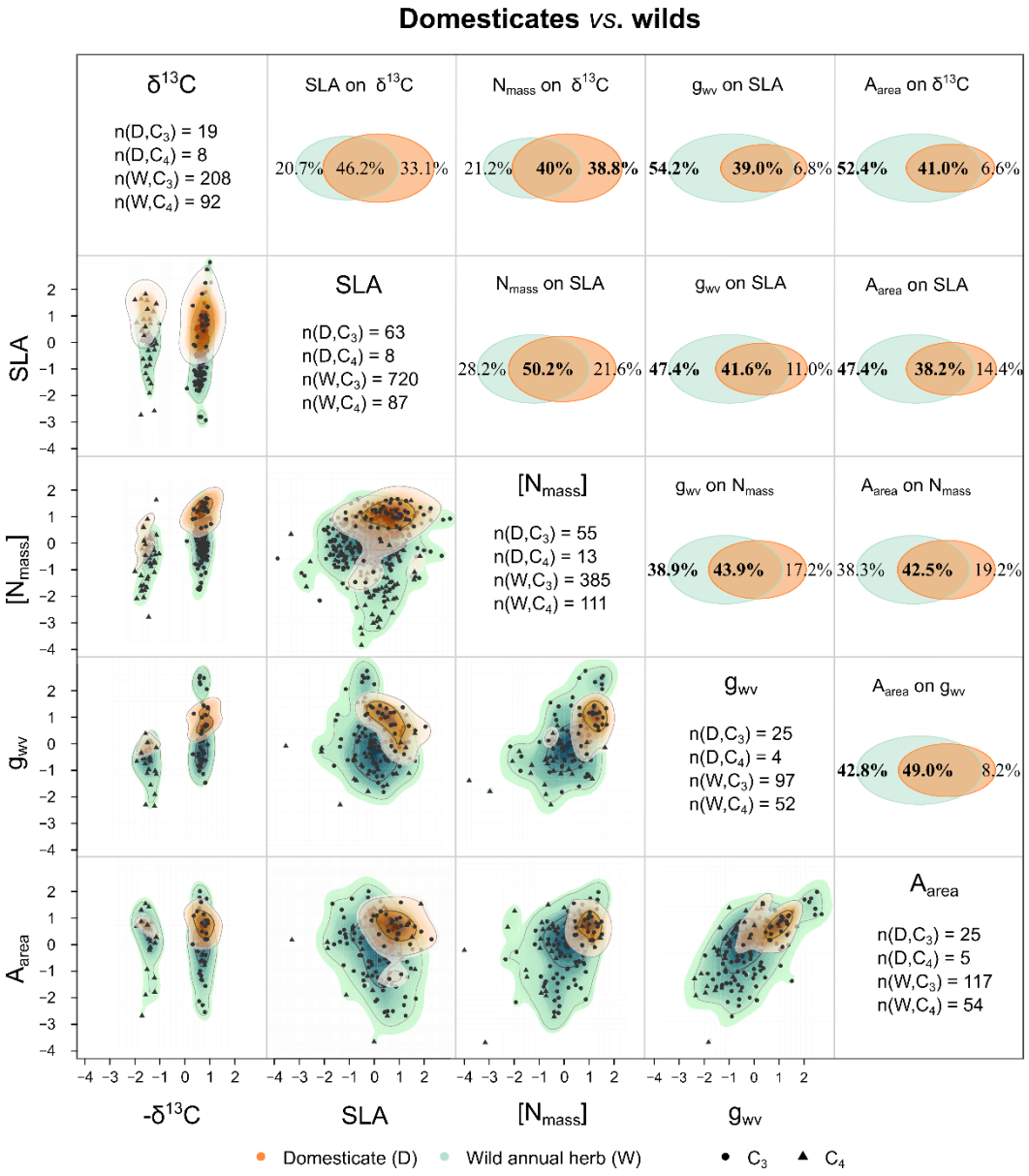

Evolution under cultivation
C3
C4
Borage
Cabbage
Faba bean
Lettuce
Oat
Okra
Peanut
Sesame
Tomato
Amaranth
Millet
Aarea
gwv
[Nmass]
SLA
δ13C
P = L
L = I
P > L *
P < L *
P
L
I

Fig. 4


Domesticates vs. wilds
δ13C
n(D,C3) = 19
n(D,C4) = 8
n(W,C3) = 208
n(W,C4) = 92
SLA on δ13C
20.7% 46.2% 33.1%
Nmass on δ13C
21.2% 40% 38.8%
gwv on SLA
54.2% 39.0% 6.8%
Aarea on δ13C
52.4% 41.0% 6.6%
SLA
n(D,C3) = 63
n(D,C4) = 8
n(W,C3) = 720
n(W,C4) = 87
Nmass on SLA
28.2% 50.2% 21.6%
gwv on SLA
47.4% 41.6% 11.0%
Aarea on SLA
47.4% 38.2% 14.4%
[Nmass]
n(D,C3) = 55
n(D,C4) = 13
n(W,C3) = 385
n(W,C4) = 111
gwv on Nmass
38.9% 43.9% 17.2%
Aarea on Nmass
38.3% 42.5% 19.2%
gwv
n(D,C3) = 25
n(D,C4) = 4
n(W,C3) = 97
n(W,C4) = 52
Aarea on gwv
42.8% 49.0% 8.2%
Aarea
n(D,C3) = 25
n(D,C4) = 5
n(W,C3) = 117
n(W,C4) = 54
SLA
[Nmass]
-4 -3 -2 -1 0 1 2
-δ13C
SLA
[Nmass]
gwv
Domesticate (D)
Wild annual herb (W)
C3
C4

SUPPLEMENTARY INFORMATION

Table S1. Range of variation in leaf ecophysiological traits and summary of data compilation. The table shows the five ecophysiological traits studied, their abbreviation, unit and range of variation, the number of individual observations and studies, and the number of domesticates (D), crops' wild progenitors (P) and wild species (W) in the *global dataset*. The total number of species does not equal the sum of domesticates, crops' wild progenitor, and wild plants, as many crops and their wild progenitors belong to the same species.

Trait	Abbr.	Unit	Range	No. of observations	No. of studies	No. of W	No. of P	No. of D
Net photosynthetic rate per unit area	A_{area}	μmol m^{-2} s^{-1}	1.41 to 48.7	3,757	62	171	22	30
Stomatal conductance to water vapour	g_{wv}	mmol m^{-2} s^{-1}	26.3 to 2,160	2,394	67	149	24	29
Mass-based leaf N concentration	$[N_{mass}]$	%	0.14 to 6.49	4,657	87	496	59	68
Specific leaf area	SLA	cm^2 g^{-1}	29.3 to 1,190.5	14,676	101	807	50	71
^{13}C isotopic composition	$\delta^{13}C$	‰	-34.3 to -10.5	894	17	300	18	27

Total no. of observations = 26,378

Total no. of studies = 194

Total no. of species = 1,147

W = 1,035

P = 69

D = 86

Table S2. Results of phylogenetic generalised least squares (PGLS) models examining the effects of early selection on ecophysiological traits for (a) the *global dataset* and for (b) indoor experiments. Photosynthetic pathway was included as a covariate. The table shows the mean (±SD) estimate, standard error (SE), *F*-statistic, degrees of freedom, and *P* value. Pagel's λ is the maximum likelihood phylogenetic signal estimated in the PGLS models across 1000 randomly resolved trees. * Binary tree provided, no polytomies to resolve. Abbreviations: A_{area}, net photosynthetic rate per unit area; g_{wv}, stomatal conductance to water vapour; $[N_{mass}]$, mass-based leaf N concentration; SLA, specific leaf area; and $\delta^{13}C$, ^{13}C isotopic composition.

			Plant type (Progenitor, Wild)					**Photosynthetic pathway** (C_3, C_4)				
		Pagel's λ	Estimate	SE	*F*	d.f.	*P*	Estimate	SE	*F*	d.f.	*P*
(a)	Global (Outdoors + Indoors)											
	A_{area}	0.67 (±0.00)	-3.73 (±0.03)	1.79 (±0.00)	4.33 (±0.06)	1,190	0.04 (±0)	1.21 (±0.02)	2.32 (±0.00)	0.27 (±0.01)	1,190	0.60 (±0)
	g_{wv}	0.91 (±0.00)	-93.7 (±1.06)	46.8 (±0.12)	3.82 (±0.07)	1,170	0.05 (±0)	-135.3 (±1.5)	68.1 (±0.31)	3.95 (±0.05)	1,170	0.05 (±0)
	$[N_{mass}]$	0.40 (±0.00)	-0.85 (±0.00)	0.13 (±0.00)	42.2 (±0.04)	1,552	0.00 (±0)	-0.43 (±0.00)	0.19 (±0.00)	5.33 (±0.01)	1,552	0.02 (±0)
	SLA	0.53 (±0.00)	-58.7 (±0.08)	15.6 (±0.01)	14.2 (±0.05)	1,854	0.00 (±0)	-17.3 (±0.41)	22.5 (±0.06)	0.59 (±0.03)	1,854	0.44 (±0)
	$\delta^{13}C$	0.81 (±0.01)	1.39 (±0.01)	0.45 (±0.00)	6.94 (±0.12)	1,315	0.01 (±0)	14.3 (±0.02)	0.48 (±0.00)	881.2 (±3.7)	1,315	0.00 (±0)
(b)	Indoors (*i.e.* under controlled experimental conditions)											
	A_{area}	0.74 (±0)	-4.45 (±0.05)	2.00 (±0.00)	4.93 (±0.09)	1,143	0.03 (±0)	0.72 (±0.04)	2.78 (±0.01)	0.07 (±0.01)	1,143	0.80 (±0)
	g_{wv}	0.93 (±0)	-111 (±1.49)	46.9 (±0.16)	5.66 (±0.12)	1,139	0.02 (±0)	-76.7 (±1.80)	73.6 (±0.57)	1.09 (±0.04)	1,139	0.30 (±0)
	$[N_{mass}]$	0.65 (±0)	-0.44 (±0.00)	0.27 (±0.00)	2.61 (±0.00)	1,116	0.11 (±0)	-0.89 (±0.00)	0.49 (±0.00)	3.29 (±0.00)	1, 116	0.07 (±0)
	SLA	0.62 (±0)	-32.7 (±0.12)	16.0 (±0.01)	4.18 (±0.03)	1,232	0.04 (±0)	-8.49 (±0.87)	31.3 (±0.08)	0.07 (±0.01)	1,232	0.79 (±0)
	$\delta^{13}C$ *	-0.30	2.14	0.44	15.1	1,19	0.00	17.3	1.00	302.2	1,1	0.00

Table S3. Results of mixed models testing the effects of domestication and improvement on ecophysiological traits. Results of linear mixed-effect models with domestication (Dom) or improvement (Imp) as dependent variable, using the *experimental dataset*. Accession nested within crop species was considered as random factor. The table shows the $F_{d.f.}$ value and significance (·, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). The variance of the models explained by the fixed effects is given by the marginal pseudo-R^2 (R^2m), and the variance explained by both the fixed and random effects is given by the conditional pseudo-R^2 (R^2c). Abbreviations: A_{area}, net photosynthetic rate per unit area; A_{mass}, net photosynthetic rate per unit mass; g_{wv}, stomatal conductance to water vapour; ETR, electron transport rate; Fv'/Fm', photosystem II photochemical efficiency; iWUE, intrinsic water-use efficiency; SLA, specific leaf area; $\delta^{13}C$, ^{13}C isotopic composition; $\delta^{15}N$, ^{15}N isotopic composition; $[N_{area}]$, area-based leaf N concentration; $[N_{mass}]$, mass-based leaf N concentration; CN, leaf C to N ratio; and PNUE, photosynthetic N use efficiency.

	Domestication (Progenitor – Landrace)			**Improvement** (Landrace – Improved)		
	Dom	**R^2m**	**R^2c**	**Imp**	**R^2m**	**R^2c**
	$F_{1,32}$			$F_{1,32}$		
A_{area}	0.89	0.003	0.48	0.00	0.000	0.56
A_{mass}	0.04	0.000	0.50	1.32	0.005	0.54
g_{wv}	0.80	0.003	0.51	0.04	0.000	0.53
ETR	0.47	0.001	0.62	0.16	0.001	0.59
Fv'/Fm'	2.13	0.006	0.50	0.24	0.001	0.62
iWUE	0.04	0.000	0.54	0.88	0.003	0.63
SLA	1.10	0.005	0.61	0.84	0.004	0.69
$\delta^{13}C$	4.56 *	0.001	0.99	0.61	0.000	0.98
$\delta^{15}N$	1.16	0.004	0.46	0.54	0.002	0.46
$[N_{area}]$	5.05 *	0.023	0.60	0.85	0.003	0.62
$[N_{mass}]$	7.14 *	0.039	0.38	0.06	0.000	0.24
CN	3.78 ·	0.014	0.36	0.74	0.003	0.34
PNUE	1.39	0.004	0.59	0.99	0.004	0.63

Table S4. Results of hypervolume analyses. Size, uniqueness and overlap in phenotypic space between domesticates (D) and wild annual herbs (W). Phenotypic spaces were constructed for all bivariate relationships between five ecophysiological traits and for each plant type (D *vs*. W). To account for differences in sample size between the two plant types and ecophysiological differences between photosynthetic pathways (C_3 *vs.* C_4), the number of wild species and the proportion of C_4 wild species was matched to that of crops ('n' and 'pct', respectively). The phenotypic spaces of wilds were generated from 1000 randomly sampled subsets, and the mean size and mean unique fraction of each phenotypic space are presented; the standard deviation is given in parentheses. Size units are the standard deviations of trait values, raised to the power of the number of dimensions (SD^2). Uniqueness refers to the fraction that is unique for each plant type in relation to the union of both phenotypic spaces. Pairwise overlaps within the two plant types were assessed as Jaccard index, and can varied between 0 and 1, which means no overlap and full overlap, respectively. Significance is the median *P*-value across all comparisons between the observed statistics and a resampled null distribution (·, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Abbreviations: A_{area}, net photosynthetic rate per unit area; g_{wv}, stomatal conductance to water vapour; [N_{mass}], mass-based leaf N concentration; SLA, specific leaf area; and $\delta^{13}C$, ^{13}C isotopic composition.

	Species sample	**Percent of C_4**	**Size**		**Uniqueness**		**Overlap**
	n	pct (%)	W (SD^2)	C (SD^2)	W	C	Jaccard index
A_{area} on g_{wv}	28	14	17 (±3)	10	0.43 (±0.09) *	0.08 (±0.06)	0.49 (±0.06) *
A_{area} on [N_{mass}]	29	14	18 (±5)	13	0.38 (±0.1) ·	0.19 (±0.08)	0.43 (±0.04) *
A_{area} on SLA	29	11	19 (±4)	11	0.47 (±0.07) **	0.14 (±0.05)	0.38 (±0.05) ***
A_{area} on $\delta^{13}C$	18	22	20 (±5)	10	0.52 (±0.1) *	0.07 (±0.07)	0.41 (±0.07) *
g_{wv} on [N_{mass}]	27	12	17 (±4)	12	0.39 (±0.09) *	0.17 (±0.08)	0.44 (±0.04) *
g_{wv} on SLA	28	11	21 (±4)	12	0.47 (±0.08) **	0.11 (±0.06)	0.42 (±0.05) **
g_{wv} on $\delta^{13}C$	17	24	19 (±4)	9	0.54 (±0.08) ***	0.07 (±0.06)	0.39 (±0.04) *
[N_{mass}] on SLA	56	13	20 (±4)	18	0.28 (±0.07) ·	0.22 (±0.07)	0.5 (±0.04) *
[N_{mass}] on $\delta^{13}C$	25	30	16 (±3)	20	0.21 (±0.05)	0.39 (±0.09) *	0.4 (±0.06) **
SLA on $\delta^{13}C$	24	27	18 (±5)	20	0.21 (±0.07)	0.33 (±0.12)	0.46 (±0.08) ·

Table S5. List of species and references used in the *global dataset*. Full list of literature sources and databases used to compile the *global* species-level *dataset* for each ecophysiological trait.

(a) Net photosynthetic rate per unit area

Species	Family	Order	Pathway	Reference	Database
Abelmoschus esculentus	Malvaceae	Malvales	C_3	This study	N.A.
Abutilon theophrasti	Malvaceae	Malvales	C_3	[1,2]	TRY
Acalypha virginica	Euphorbiaceae	Malpighiales	C_3	[3]	TRY
Aconitum gymnandrum	Ranunculaceae	Ranunculales	C_3	[4]	TRY
				[5]	BIEN
Aegilops cylindrica	Poaceae	Poales	C_3	[6]	TRY
Aegilops geniculata	Poaceae	Poales	C_3	[2]	TRY
Aegilops triuncialis	Poaceae	Poales	C_3	[7]	BIEN
Aeluropus littoralis	Poaceae	Poales	C_4	[6]	TRY
Agriophyllum squarrosum	Amaranthaceae	Caryophyllales	C_4	[2]	TRY
Agrostis inaequiglumis	Poaceae	Poales	C_3	[6]	TRY
Agrostis lachnantha	Poaceae	Poales	C_3	[6]	TRY
Agrostis scabra	Poaceae	Poales	C_3	[2,8,9]	TRY
Aira caryophyllea	Poaceae	Poales	C_3	[7]	BIEN
Alopecurus carolinianus	Poaceae	Poales	C_3	[6]	TRY
Alopecurus myosuroides	Poaceae	Poales	C_3	[6]	TRY
Alopecurus utriculatus	Poaceae	Poales	C_3	[6]	TRY
Amaranthus blitoides	Amaranthaceae	Caryophyllales	C_4	[2,10]	TRY
Amaranthus cruentus	Amaranthaceae	Caryophyllales	C_4	This study	N.A.
Amaranthus retroflexus	Amaranthaceae	Caryophyllales	C_4	[1,2,10]	TRY
Anthyllis vulneraria	Fabaceae	Fabales	C_3	[11]	TRY
Apera spica-venti	Poaceae	Poales	C_3	[12,13]	TRY

Arabidopsis thaliana	Brassicaceae	Brassicales	C_3	[14–16]	TRY
				[17–21]	N.A.
Arachis hypogaea	Fabaceae	Fabales	C_3	This study	N.A.
Arachis monticola	Fabaceae	Fabales	C_3	This study	N.A.
Aristida oligantha	Poaceae	Poales	C_4	[10]	TRY
Artemisia annua	Asteraceae	Asterales	C_3	[2]	TRY
Artemisia scoparia	Asteraceae	Asterales	C_3	[2]	TRY
Arthraxon hispidus	Poaceae	Poales	C_4	[2]	TRY
Atriplex hortensis	Amaranthaceae	Caryophyllales	C_4	[16]	TRY
Atriplex laevis	Amaranthaceae	Caryophyllales	C_4	[2]	TRY
Atriplex oblongifolia	Amaranthaceae	Caryophyllales	C_4	[2]	TRY
Avena barbata	Poaceae	Poales	C_3	[1]	TRY
				[7]	BIEN
Avena fatua	Poaceae	Poales	C_3	[12,13,22]	TRY
				[7]	BIEN
Avena sativa	Poaceae	Poales	C_3	This study	N.A.
				[7]	BIEN
Avena sterilis	Poaceae	Poales	C_3	This study	N.A.
Axyris amaranthoides	Amaranthaceae	Caryophyllales	C_4	[23]	TRY
Beckmannia syzigachne	Poaceae	Poales	C_3	[6]	TRY
Beta vulgaris	Amaranthaceae	Caryophyllales	C_3	[24,25]	N.A.
				[2,16]	TRY
Bidens cernua	Asteraceae	Asterales	C_3	[26]	TRY
Bidens frondosa	Asteraceae	Asterales	C_3	[26]	TRY
Borago officinalis	Boraginaceae	Boraginales	C_3	This study	N.A.
Bothriochloa pertusa	Poaceae	Poales	C_4	[27]	China Plant Trait
Brachiaria eruciformis	Poaceae	Poales	C_4	[6]	TRY
Brachiaria mollis	Poaceae	Poales	C_3	[6]	TRY

Brachiaria platyphylla	Poaceae	Poales	C_4	[6]	TRY
Brachiaria ruziziensis	Poaceae	Poales	C_4	[6]	TRY
Brachypodium distachyon	Poaceae	Poales	C_3	[1,2]	TRY
Brassica napus	Brassicaceae	Brassicales	C_3	[28–31]	N.A.
				[32]	TRY
Brassica oleracea	Brassicaceae	Brassicales	C_3	[32]	TRY
				[25]	N.A.
				This study	N.A.
Brassica rapa	Brassicaceae	Brassicales	C_3	[1]	TRY
Briza maxima	Poaceae	Poales	C_3	[33]	AusTraits
				[7]	BIEN
Bromus alopecuros	Poaceae	Poales	C_3	[6]	TRY
Bromus carinatus	Poaceae	Poales	C_3	[6]	TRY
				[7]	BIEN
Bromus danthoniae	Poaceae	Poales	C_3	[6]	TRY
Bromus diandrus	Poaceae	Poales	C_3	[7]	BIEN
Bromus hordeaceus	Poaceae	Poales	C_3	[1,12,13]	TRY
				[7]	BIEN
Bromus intermedius	Poaceae	Poales	C_3	[6]	TRY
Bromus japonicus	Poaceae	Poales	C_3	[6]	TRY
Bromus lanceolatus	Poaceae	Poales	C_3	[2,6]	TRY
Bromus madritensis	Poaceae	Poales	C_3	[1]	TRY
Bromus pectinatus	Poaceae	Poales	C_3	[6]	TRY
Bromus sterilis	Poaceae	Poales	C_3	[12,13]	TRY
Campanula americana	Campanulaceae	Asterales	C_3	[34]	TRY
Capsicum annuum	Solanaceae	Solanales	C_3	[16]	TRY
				[35]	N.A.
Cenchrus echinatus	Poaceae	Poales	C_4	[6]	TRY

Centaurea cyanus	Asteraceae	Asterales	C_3	[3,34]	TRY
Cerastium glomeratum	Caryophyllaceae	Caryophyllales	C_3	[13]	TRY
Chamaecrista fasciculata	Fabaceae	Fabales	C_3	[10]	TRY
Chenopodium acuminatum	Amaranthaceae	Caryophyllales	C_3	[2]	TRY
Chloris radiata	Poaceae	Poales	C_4	[6]	TRY
Chloris virgata	Poaceae	Poales	C_4	[2]	TRY
Chylismia brevipes	Onagraceae	Myrtales	C_3	[2]	TRY
Chylismia claviformis	Onagraceae	Myrtales	C_3	[2]	TRY
Corispermum mongolicum	Amaranthaceae	Caryophyllales	C_3	[2]	TRY
Crassocephalum crepidioides	Asteraceae	Asterales	C_3	[22]	TRY
Crepis capillaris	Asteraceae	Asterales	C_3	[12,13]	TRY
Cucumis sativus	Cucurbitaceae	Cucurbitales	C_3	[36]	N.A.
				[16]	TRY
Cynosurus echinatus	Poaceae	Poales	C_3	[7]	BIEN
Cyperus diandrus	Cyperaceae	Poales	C_4	[26]	TRY
Cyperus flavidus	Cyperaceae	Poales	C_4	[37]	TRY
Cyperus reduncus	Cyperaceae	Poales	C_4	[26]	TRY
Cypripedium flavum	Orchidaceae	Asparagales	C_3	[16]	TRY
Dactyloctenium aegyptium	Poaceae	Poales	C_4	[6]	TRY
Dactyloctenium radulans	Poaceae	Poales	C_4	[32]	TRY
Danthoniopsis dinteri	Poaceae	Poales	C_4	[6]	TRY
Digitaria bicornis	Poaceae	Poales	C_4	[6]	TRY
Digitaria ciliaris	Poaceae	Poales	C_4	[6]	TRY
Digitaria debilis	Poaceae	Poales	C_4	[6]	TRY
Digitaria eriostachya	Poaceae	Poales	C_4	[6]	TRY
Digitaria ischaemum	Poaceae	Poales	C_4	[3,6,26]	TRY
Digitaria setigera	Poaceae	Poales	C_4	[6]	TRY
Digitaria ternata	Poaceae	Poales	C_4	[6]	TRY

Digitaria violascens	Poaceae	Poales	C_4	[6]	TRY
Diplotaxis ibicensis	Brassicaceae	Brassicales	C_3	[24]	N.A.
				[16]	TRY
Echinaria capitata	Poaceae	Poales	C_3	[6]	TRY
Echinochloa muricata	Poaceae	Poales	C_4	[6]	TRY
Echium plantagineum	Boraginaceae	Boraginales	C_3	[16]	TRY
Ehrharta longiflora	Poaceae	Poales	C_3	[6]	TRY
Eleocharis obtusa	Cyperaceae	Poales	C_3	[26]	TRY
Eleusine coracana	Poaceae	Poales	C_4	[6]	TRY
Eleusine indica	Poaceae	Poales	C_4	[6,10]	TRY
Eleusine tristachya	Poaceae	Poales	C_4	[6]	TRY
Enneapogon gracilis	Poaceae	Poales	C_4	[6]	TRY
Enneapogon lindleyanus	Poaceae	Poales	C_4	[6]	TRY
Eragrostis macilenta	Poaceae	Poales	C_4	[6]	TRY
Eragrostis minor	Poaceae	Poales	C_4	[6]	TRY
Eragrostis neesii	Poaceae	Poales	C_4	[6]	TRY
Eragrostis patentipilosa	Poaceae	Poales	C_4	[6]	TRY
Eragrostis pectinacea	Poaceae	Poales	C_4	[6,10,26]	TRY
Eragrostis pilosa	Poaceae	Poales	C_4	[6]	TRY
Eragrostis porosa	Poaceae	Poales	C_4	[6]	TRY
Eremopyrum triticeum	Poaceae	Poales	C_3	[6]	TRY
Erigeron annuus	Asteraceae	Asterales	C_3	[10]	TRY
Eriochloa contracta	Poaceae	Poales	C_3	[6]	TRY
Euphorbia helioscopia	Euphorbiaceae	Malpighiales	C_3	[2]	TRY
Euphorbia humifusa	Euphorbiaceae	Malpighiales	C_4	[2]	TRY
Euphorbia nutans	Euphorbiaceae	Malpighiales	C_4	[10]	TRY
Festuca incurva	Poaceae	Poales	C_3	[6]	TRY
Gastridium ventricosum	Poaceae	Poales	C_3	[6]	TRY

Glycine max	Fabaceae	Fabales	C_3	[20,38]	N.A.
				[1,16]	TRY
Gnaphalium affine	Asteraceae	Asterales	C_3	[2,4]	TRY
Gnaphalium luteoalbum	Asteraceae	Asterales	C_3	[5]	BIEN
Grubovia dasyphylla	Amaranthaceae	Caryophyllales	C_4	[2]	TRY
Helianthus agrestis	Asteraceae	Asterales	C_3	[39]	BIEN
Helianthus annuus	Asteraceae	Asterales	C_3	[1,10,16]	TRY
				[39]	BIEN
				[25,35,40]	N.A.
Helianthus argophyllus	Asteraceae	Asterales	C_3	[39]	BIEN
Helianthus debilis	Asteraceae	Asterales	C_3	[39]	BIEN
Helianthus neglectus	Asteraceae	Asterales	C_3	[39]	BIEN
Helianthus praecox	Asteraceae	Asterales	C_3	[39]	BIEN
Hordeum murinum	Poaceae	Poales	C_3	[1]	TRY
Hordeum pusillum	Poaceae	Poales	C_3	[6,10]	TRY
Hordeum vulgare	Poaceae	Poales	C_3	[1]	TRY
Impatiens capensis	Balsaminaceae	Ericales	C_3	[37]	TRY
Impatiens noli-tangere	Balsaminaceae	Ericales	C_3	[2]	TRY
Impatiens rubrostriata	Balsaminaceae	Ericales	C_3	[22]	TRY
Iseilema macratherum	Poaceae	Poales	C_4	[6]	TRY
Jacobaea vulgaris	Asteraceae	Asterales	C_3	[12,13]	TRY
Kali collinum	Amaranthaceae	Caryophyllales	C_4	[2,23]	TRY
Kalimeris altaica	Asteraceae	Asterales	C_3	[2]	TRY
Lactuca canadensis	Asteraceae	Asterales	C_3	[10]	TRY
Lactuca ludoviciana	Asteraceae	Asterales	C_3	[2,10]	TRY
Lactuca sativa	Asteraceae	Asterales	C_3	This study	N.A.
Lactuca serriola	Asteraceae	Asterales	C_3	This study	N.A.
Lapsana communis	Asteraceae	Asterales	C_3	[12,13]	TRY

Lepidium densiflorum	Brassicaceae	Brassicales	C_3	[10]	TRY
Leptochloa fusca	Poaceae	Poales	C_4	[6]	TRY
Lipandra polysperma	Amaranthaceae	Caryophyllales	C_3	[3,26,34]	TRY
Lolium canariense	Poaceae	Poales	C_3	[6]	TRY
Lolium persicum	Poaceae	Poales	C_3	[6]	TRY
Lolium rigidum	Poaceae	Poales	C_3	[1,6]	TRY
Lotus corniculatus	Fabaceae	Fabales	C_3	[11–13]	TRY
Matricaria chamomilla	Asteraceae	Asterales	C_3	[12,13]	TRY
Melanocenchris abyssinica	Poaceae	Poales	C_3	[6]	TRY
Melinis repens	Poaceae	Poales	C_4	[2]	TRY
Mentha spicata	Lamiaceae	Lamiales	C_3	[16]	TRY
Microstegium vimineum	Poaceae	Poales	C_4	[6,37]	TRY
Muhlenbergia microsperma	Poaceae	Poales	C_4	[6]	TRY
Myagrum perfoliatum	Brassicaceae	Brassicales	C_3	[34]	TRY
Nepeta tenuifolia	Lamiaceae	Lamiales	C_3	[2]	TRY
Nigella damascena	Ranunculaceae	Ranunculales	C_3	[34]	TRY
Ocimum basilicum	Lamiaceae	Lamiales	C_3	[16]	TRY
				[35]	N.A.
Ophiuros exaltatus	Poaceae	Poales	C_4	[6]	TRY
Oryza barthii	Poaceae	Poales	C_3	[16]	TRY
Oryza brachyantha	Poaceae	Poales	C_3	[16]	TRY
Oryza latifolia	Poaceae	Poales	C_3	[16]	TRY
				[41]	N.A.
Oryza minuta	Poaceae	Poales	C_3	[16]	TRY
Oryza officinalis	Poaceae	Poales	C_3	[16]	TRY
Oryza punctata	Poaceae	Poales	C_3	[16]	TRY
				[41]	N.A.
Oryza rufipogon	Poaceae	Poales	C_3	[16]	TRY

				[41]	N.A.
Oryza sativa	Poaceae	Poales	C_3	[20,36,40–53]	N.A.
				[1,16,54]	TRY
Oxybasis glauca	Amaranthaceae	Caryophyllales	C_4	[2,23]	TRY
Panicum bisulcatum	Poaceae	Poales	C_3	[6]	TRY
Panicum capillare	Poaceae	Poales	C_4	[2,3,10,26]	TRY
Panicum dichotomiflorum	Poaceae	Poales	C_4	[6]	TRY
Panicum laevinode	Poaceae	Poales	C_4	[6]	TRY
Panicum schinzii	Poaceae	Poales	C_4	[6]	TRY
Papaver dubium	Papaveraceae	Ranunculales	C_3	[12,13]	TRY
Pennisetum glaucum	Poaceae	Poales	C_4	[3,10]	TRY
				This study	N.A.
Perotis patens	Poaceae	Poales	C_4	[6]	TRY
Persicaria bungeana	Polygonaceae	Caryophyllales	C_3	[2,26]	TRY
Persicaria lapathifolia	Polygonaceae	Caryophyllales	C_3	[2,26]	TRY
Phalaris canariensis	Poaceae	Poales	C_3	[6]	TRY
Phaseolus vulgaris	Fabaceae	Fabales	C_3	[35,55,56]	N.A.
				[1,16]	TRY
Phleum boissieri	Poaceae	Poales	C_3	[6]	TRY
Phoebanthus tenuifolius	Asteraceae	Asterales	C_3	[39]	BIEN
Pisum sativum	Fabaceae	Fabales	C_3	[25]	N.A.
Plantago major	Plantaginaceae	Lamiales	C_3	[2,3,12,13,15,16,26,57]	TRY
Poa annua	Poaceae	Poales	C_3	[1,13,16,57]	TRY
Polypogon monspeliensis	Poaceae	Poales	C_3	[6]	TRY
Raphanus raphanistrum	Brassicaceae	Brassicales	C_3	[1,12,13,16]	TRY
Rostraria cristata	Poaceae	Poales	C_3	[2–4,23]	TRY
				[5]	BIEN
Rudbeckia hirta	Asteraceae	Asterales	C_3	[10]	TRY

Secale cereale	Poaceae	Poales	C_3	[16]	TRY
Sesamum indicum	Pedaliaceae	Lamiales	C_3	This study	N.A.
Setaria plicata	Poaceae	Poales	C_4	[27]	China Plant Trait
Setaria viridis	Poaceae	Poales	C_4	[2,3,6]	TRY
Sigesbeckia orientalis	Asteraceae	Asterales	C_3	[58]	AusTraits
Solanum lycopersicum	Solanaceae	Solanales	C_3	[25,59]	N.A.
				[1,16]	TRY
				[60]	BIEN
				This study	N.A.
Solanum pimpinellifolium	Solanaceae	Solanales	C_3	[25]	N.A.
				[60]	BIEN
				This study	N.A.
Solanum rostratum	Solanaceae	Solanales	C_3	[10]	TRY
Sonchus asper	Asteraceae	Asterales	C_3	[12,13]	TRY
Sphenopholis obtusata	Poaceae	Poales	C_3	[6]	TRY
Spinacia oleracea	Amaranthaceae	Caryophyllales	C_3	[16]	TRY
				[35,52]	N.A.
Suaeda glauca	Amaranthaceae	Caryophyllales	C_4	[2]	TRY
Taeniatherum caputmedusae	Poaceae	Poales	C_3	[7]	BIEN
Tragus australianus	Poaceae	Poales	C_4	[32]	TRY
Tragus berteronianus	Poaceae	Poales	C_4	[2]	TRY
Tribulus terrestris	Zygophyllaceae	Zygophyllales	C_4	[2]	TRY
Trifolium repens	Fabaceae	Fabales	C_3	[2,11–13]	TRY
Trigonella alba	Fabaceae	Fabales	C_3	[2,34]	TRY
Trigonella officinalis	Fabaceae	Fabales	C_3	[2,3]	TRY
Tripleurospermum inodorum	Asteraceae	Asterales	C_4	[12,13]	TRY
Triticum aestivum	Poaceae	Poales	C_3	[20,36,52,61–65]	N.A.
				[1,16,32,66]	TRY

Triticum dicoccoides	Poaceae	Poales	C_3	[25]	N.A.
Triticum turgidum	Poaceae	Poales	C_3	[16,66]	TRY
				[25]	N.A.
Urochloa brachyura	Poaceae	Poales	C_4	[6]	TRY
Veronica arvensis	Plantaginaceae	Lamiales	C_3	[12,13]	TRY
Vicia faba	Fabaceae	Fabales	C_3	[1,16]	TRY
				This study	N.A.
Vicia narbonensis	Fabaceae	Fabales	C_3	This study	N.A.
Vulpia bromoides	Poaceae	Poales	C_3	[12,13]	TRY
Vulpia microstachys	Poaceae	Poales	C_3	[7]	BIEN
Vulpia myuros	Poaceae	Poales	C_3	[7]	BIEN
Vulpia octoflora	Poaceae	Poales	C_3	[10]	TRY
Whiteochloa capillipes	Poaceae	Poales	C_4	[6]	TRY
Xanthium orientale	Asteraceae	Asterales	C_3	[16]	TRY
Xanthium strumarium	Asteraceae	Asterales	C_3	[2,10,16,26]	TRY
Zea mays	Poaceae	Poales	C_4	[16,66]	TRY
Zingeria biebersteiniana	Poaceae	Poales	C_3	[6]	TRY
Zornia glochidiata	Fabaceae	Fabales	C_3	[67]	TRY

(b) Stomatal conductance to water

Species	Family	Order	Type	Reference	Database
Abelmoschus esculentus	Malvaceae	Malvales	C_3	This study	N.A.
Aegilops cylindrica	Poaceae	Poales	C_3	[6]	TRY
Aeluropus littoralis	Poaceae	Poales	C_4	[6]	TRY
Agrostis inaequiglumis	Poaceae	Poales	C_3	[6]	TRY
Agrostis lachnantha	Poaceae	Poales	C_3	[6]	TRY
Agrostis scabra	Poaceae	Poales	C_3	[2]	TRY
Alopecurus carolinianus	Poaceae	Poales	C_3	[6]	TRY
Alopecurus myosuroides	Poaceae	Poales	C_3	[6]	TRY
Alopecurus utriculatus	Poaceae	Poales	C_3	[6]	TRY
Amaranthus blitoides	Amaranthaceae	Caryophyllales	C_4	[2,10]	TRY
Amaranthus cruentus	Amaranthaceae	Caryophyllales	C_4	This study	N.A.
Amaranthus retroflexus	Amaranthaceae	Caryophyllales	C_4	[2,10,16]	TRY
Apera spica-venti	Poaceae	Poales	C_3	[12,13]	TRY
Arabidopsis thaliana	Brassicaceae	Brassicales	C_3	[15,16]	TRY
				[18,19,21,68,69]	N.A.
Arachis hypogaea	Fabaceae	Fabales	C_3	This study	N.A.
Arachis monticola	Fabaceae	Fabales	C_3	This study	N.A.
Aristida oligantha	Poaceae	Poales	C_4	[10]	TRY
Avena fatua	Poaceae	Poales	C_3	[12,13,22]	TRY
Avena sativa	Poaceae	Poales	C_3	This study	N.A.
Avena sterilis	Poaceae	Poales	C_3	This study	N.A.
Axyris amaranthoides	Amaranthaceae	Caryophyllales	C_4	[23]	TRY
Beckmannia syzigachne	Poaceae	Poales	C_3	[6]	TRY
Beta vulgaris	Amaranthaceae	Caryophyllales	C_3	[25,70]	N.A.
				[2,16]	TRY
Bidens cernua	Asteraceae	Asterales	C_3	[26]	TRY
Bidens frondosa	Asteraceae	Asterales	C_3	[26]	TRY
Borago officinalis	Boraginaceae	Boraginales	C_3	This study	N.A.

Bothriochloa pertusa	Poaceae	Poales	C_4	[27]	China Plant Trait
Brachiaria eruciformis	Poaceae	Poales	C_4	[6]	TRY
Brachiaria mollis	Poaceae	Poales	C_3	[6]	TRY
Brachiaria platyphylla	Poaceae	Poales	C_4	[6]	TRY
Brachiaria ruziziensis	Poaceae	Poales	C_4	[6]	TRY
Brassica napus	Brassicaceae	Brassicales	C_3	[28,29,31,36]	N.A.
				[32]	TRY
Brassica oleracea	Brassicaceae	Brassicales	C_3	[32]	TRY
				[6,25]	N.A.
				This study	N.A.
Bromus alopecuros	Poaceae	Poales	C_3	[6]	TRY
Bromus carinatus	Poaceae	Poales	C_3	[6]	TRY
Bromus danthoniae	Poaceae	Poales	C_3	[6]	TRY
Bromus hordeaceus	Poaceae	Poales	C_3	[12,13,71]	TRY
Bromus intermedius	Poaceae	Poales	C_3	[6]	TRY
Bromus japonicus	Poaceae	Poales	C_3	[6]	TRY
Bromus lanceolatus	Poaceae	Poales	C_3	[6]	TRY
Bromus pectinatus	Poaceae	Poales	C_3	[6]	TRY
Bromus sterilis	Poaceae	Poales	C_3	[12,13]	TRY
Campanula americana	Campanulaceae	Asterales	C_3	[34]	TRY
Capsicum annuum	Solanaceae	Solanales	C_3	[35,72]	N.A.
				[16]	TRY
Cenchrus echinatus	Poaceae	Poales	C_4	[6]	TRY
Centaurea cyanus	Asteraceae	Asterales	C_3	[34]	TRY
Cerastium glomeratum	Caryophyllaceae	Caryophyllales	C_3	[13]	TRY
Chamaecrista fasciculata	Fabaceae	Fabales	C_3	[10]	TRY
Chloris radiata	Poaceae	Poales	C_4	[6]	TRY
Chylismia claviformis	Onagraceae	Myrtales	C_3	[16]	TRY
Crassocephalum crepidioides	Asteraceae	Asterales	C_3	[22]	TRY
Crepis biennis	Asteraceae	Asterales	C_3	[71]	TRY
Crepis capillaris	Asteraceae	Asterales	C_3	[12,13]	TRY

Cucumis sativus	Cucurbitaceae	Cucurbitales	C_3	[36,73]	N.A.
				[16]	TRY
Cyperus diandrus	Cyperaceae	Poales	C_4	[26]	TRY
Cyperus flavidus	Cyperaceae	Poales	C_4	[37]	TRY
Cyperus reduncus	Cyperaceae	Poales	C_4	[26]	TRY
Cypripedium flavum	Orchidaceae	Asparagales	C_3	[16,74]	TRY
Dactyloctenium aegyptium	Poaceae	Poales	C_4	[6]	TRY
Dactyloctenium radulans	Poaceae	Poales	C_4	[32]	TRY
Danthoniopsis dinteri	Poaceae	Poales	C_4	[6]	TRY
Digitaria bicornis	Poaceae	Poales	C_4	[6]	TRY
Digitaria ciliaris	Poaceae	Poales	C_4	[6]	TRY
Digitaria debilis	Poaceae	Poales	C_4	[6]	TRY
Digitaria eriostachya	Poaceae	Poales	C_4	[6]	TRY
Digitaria ischaemum	Poaceae	Poales	C_4	[6,26]	TRY
Digitaria setigera	Poaceae	Poales	C_4	[6]	TRY
Digitaria ternata	Poaceae	Poales	C_4	[6]	TRY
Digitaria violascens	Poaceae	Poales	C_4	[6]	TRY
Diplotaxis ibicensis	Brassicaceae	Brassicales	C_3	[70]	N.A.
				[16]	TRY
Echinaria capitata	Poaceae	Poales	C_3	[6]	TRY
Echinochloa muricata	Poaceae	Poales	C_4	[6]	TRY
Ehrharta longiflora	Poaceae	Poales	C_3	[6]	TRY
Eleocharis obtusa	Cyperaceae	Poales	C_3	[26]	TRY
Eleusine coracana	Poaceae	Poales	C_4	[6]	TRY
Eleusine indica	Poaceae	Poales	C_4	[6,10]	TRY
Eleusine tristachya	Poaceae	Poales	C_4	[6]	TRY
Enneapogon gracilis	Poaceae	Poales	C_4	[6]	TRY
Enneapogon lindleyanus	Poaceae	Poales	C_4	[6]	TRY
Eragrostis macilenta	Poaceae	Poales	C_4	[6]	TRY
Eragrostis minor	Poaceae	Poales	C_4	[6]	TRY
Eragrostis neesii	Poaceae	Poales	C_4	[6]	TRY

Eragrostis patentipilosa	Poaceae	Poales	C_4	6	TRY
Eragrostis pectinacea	Poaceae	Poales	C_4	6,10,26	TRY
Eragrostis pilosa	Poaceae	Poales	C_4	6	TRY
Eragrostis porosa	Poaceae	Poales	C_4	6	TRY
Eremopyrum triticeum	Poaceae	Poales	C_3	6	TRY
Erigeron annuus	Asteraceae	Asterales	C_3	10	TRY
Eriochloa contracta	Poaceae	Poales	C_3	6	TRY
Euphorbia nutans	Euphorbiaceae	Malpighiales	C_4	10	TRY
Festuca incurva	Poaceae	Poales	C_3	6	TRY
Gastridium ventricosum	Poaceae	Poales	C_3	6	TRY
Gentianella amarella	Gentianaceae	Gentianales	C_3	75	TRY
Glycine max	Fabaceae	Fabales	C_3	38,76	N.A.
				16,77	TRY
Helianthus agrestis	Asteraceae	Asterales	C_3	39	BIEN
Helianthus annuus	Asteraceae	Asterales	C_3	39	BIEN
				25,35,40	N.A.
				10,16	TRY
Helianthus argophyllus	Asteraceae	Asterales	C_3	39	BIEN
Helianthus debilis	Asteraceae	Asterales	C_3	39	BIEN
Helianthus neglectus	Asteraceae	Asterales	C_3	39	BIEN
Helianthus praecox	Asteraceae	Asterales	C_3	39	BIEN
Hordeum pusillum	Poaceae	Poales	C_3	6,10	TRY
Hordeum vulgare	Poaceae	Poales	C_3	78	N.A.
Impatiens capensis	Balsaminaceae	Ericales	C_3	37	TRY
Impatiens noei	Balsaminaceae	Ericales	C_3	79	N.A.
Impatiens rubrostriata	Balsaminaceae	Ericales	C_3	22	TRY
Iseilema macratherum	Poaceae	Poales	C_4	6	TRY
Jacobaea vulgaris	Asteraceae	Asterales	C_3	12,13	TRY
Kali collinum	Amaranthaceae	Caryophyllales	C_4	23	TRY
Lactuca canadensis	Asteraceae	Asterales	C_3	10	TRY
Lactuca ludoviciana	Asteraceae	Asterales	C_3	10	TRY

Lactuca sativa	Asteraceae	Asterales	C_3	This study	N.A.
Lactuca serriola	Asteraceae	Asterales	C_3	This study	N.A.
Lapsana communis	Asteraceae	Asterales	C_3	[12,13]	TRY
Lepidium densiflorum	Brassicaceae	Brassicales	C_3	[10]	TRY
Leptochloa fusca	Poaceae	Poales	C_4	[6]	TRY
Lipandra polysperma	Amaranthaceae	Caryophyllales	C_3	[26,34]	TRY
Lolium canariense	Poaceae	Poales	C_3	[6]	TRY
Lolium persicum	Poaceae	Poales	C_3	[6]	TRY
Lolium rigidum	Poaceae	Poales	C_3	[6]	TRY
Lotus corniculatus	Fabaceae	Fabales	C_3	[12,13,71]	TRY
Matricaria chamomilla	Asteraceae	Asterales	C_3	[12,13]	TRY
Melanocenchris abyssinica	Poaceae	Poales	C_3	[6]	TRY
Mentha spicata	Lamiaceae	Lamiales	C_3	[80]	N.A.
				[16]	TRY
Mercurialis annua	Euphorbiaceae	Malpighiales	C_3	[79]	N.A.
Micropyrum tenellum	Poaceae	Poales	C_3	[81]	N.A.
Microstegium vimineum	Poaceae	Poales	C_4	[6,37]	TRY
Muhlenbergia microsperma	Poaceae	Poales	C_4	[6]	TRY
Myagrum perfoliatum	Brassicaceae	Brassicales	C_3	[34]	TRY
Nicotiana plumbaginifolia	Solanaceae	Solanales	C_3	[82]	N.A.
Nigella damascena	Ranunculaceae	Ranunculales	C_3	[34]	TRY
Ocimum basilicum	Lamiaceae	Lamiales	C_3	[16]	TRY
				[35]	N.A.
Ophiuros exaltatus	Poaceae	Poales	C_4	[6]	TRY
Oryza barthii	Poaceae	Poales	C_3	[16]	TRY
Oryza brachyantha	Poaceae	Poales	C_3	[16]	TRY
Oryza latifolia	Poaceae	Poales	C_3	[16]	TRY
				[41]	N.A.
Oryza minuta	Poaceae	Poales	C_3	[16]	TRY
Oryza officinalis	Poaceae	Poales	C_3	[16]	TRY
Oryza punctata	Poaceae	Poales	C_3	[16]	TRY

Oryza punctata	Poaceae	Poales	C_3	[41]	N.A.
Oryza rufipogon	Poaceae	Poales	C_3	[16]	TRY
				[41,83]	N.A.
Oryza sativa	Poaceae	Poales	C_3	[36,40–43,46,48,50,51,84,85]	N.A.
				[16]	TRY
Oxybasis glauca	Amaranthaceae	Caryophyllales	C_4	[23]	TRY
Panicum bisulcatum	Poaceae	Poales	C_3	[6]	TRY
Panicum capillare	Poaceae	Poales	C_4	[2,10,26]	TRY
Panicum dichotomiflorum	Poaceae	Poales	C_4	[6]	TRY
Panicum laevinode	Poaceae	Poales	C_4	[6]	TRY
Panicum schinzii	Poaceae	Poales	C_4	[6]	TRY
Papaver dubium	Papaveraceae	Ranunculales	C_3	[12,13]	TRY
Pennisetum glaucum	Poaceae	Poales	C_4	This study	N.A.
				[10]	TRY
Perotis patens	Poaceae	Poales	C_4	[6]	TRY
Persicaria bungeana	Polygonaceae	Caryophyllales	C_3	[26]	TRY
Persicaria lapathifolia	Polygonaceae	Caryophyllales	C_3	[26]	TRY
Phalaris canariensis	Poaceae	Poales	C_3	[6]	TRY
Phaseolus vulgaris	Fabaceae	Fabales	C_3	[35,55,56,86]	N.A.
				[16,54]	TRY
Phleum boissieri	Poaceae	Poales	C_3	[6]	TRY
Phoebanthus tenuifolius	Asteraceae	Asterales	C_3	[39]	BIEN
Pisum sativum	Fabaceae	Fabales	C_3	[25]	N.A.
Plantago major	Plantaginaceae	Lamiales	C_3	[12,13,15,26]	TRY
Poa annua	Poaceae	Poales	C_3	[13]	TRY
Polypogon monspeliensis	Poaceae	Poales	C_3	[6]	TRY
Raphanus raphanistrum	Brassicaceae	Brassicales	C_3	[12,13]	TRY
Rostraria cristata	Poaceae	Poales	C_3	[2,23]	TRY
Rudbeckia hirta	Asteraceae	Asterales	C_3	[10]	TRY
Rumex dentatus	Polygonaceae	Caryophyllales	C_3	[87]	N.A.
Secale cereale	Poaceae	Poales	C_3	[16]	TRY

Sesamum indicum	Pedaliaceae	Lamiales	C_3	This study	N.A.
Setaria plicata	Poaceae	Poales	C_4	[27]	China Plant Trait
Setaria viridis	Poaceae	Poales	C_4	[6]	TRY
Sigesbeckia orientalis	Asteraceae	Asterales	C_3	[58]	AusTraits
Solanum lycopersicum	Solanaceae	Solanales	C_3	[25,59,88]	N.A.
				[60]	BIEN
				[16]	TRY
				This study	N.A.
Solanum pimpinellifolium	Solanaceae	Solanales	C_3	[25]	N.A.
				[60]	BIEN
				This study	N.A.
Solanum rostratum	Solanaceae	Solanales	C_3	[10]	TRY
Sonchus asper	Asteraceae	Asterales	C_3	[12,13]	TRY
Sorghum bicolor	Poaceae	Poales	C_4	[16]	TRY
Sphenopholis obtusata	Poaceae	Poales	C_3	[6]	TRY
Spinacia oleracea	Amaranthaceae	Caryophyllales	C_3	[16]	TRY
				[35]	N.A.
Tragus australianus	Poaceae	Poales	C_4	[32]	TRY
Trifolium campestre	Fabaceae	Fabales	C_3	[71]	TRY
Trifolium repens	Fabaceae	Fabales	C_3	[12,13,71]	TRY
Trigonella alba	Fabaceae	Fabales	C_3	[34]	TRY
Tripleurospermum inodorum	Asteraceae	Asterales	C_4	[12,13]	TRY
Triticum aestivum	Poaceae	Poales	C_3	[36,61,63–65,86]	N.A.
				[32]	TRY
Triticum dicoccoides	Poaceae	Poales	C_3	[25]	N.A.
Triticum turgidum	Poaceae	Poales	C_3	[25,89]	N.A.
				[16]	TRY
Urochloa brachyura	Poaceae	Poales	C_4	[6]	TRY
Veronica arvensis	Plantaginaceae	Lamiales	C_3	[12,13]	TRY
Vicia faba	Fabaceae	Fabales	C_3	[81]	N.A.
				[16]	TRY

				This study	N.A.
Vicia narbonensis	Fabaceae	Fabales	C_3	This study	N.A.
Vulpia bromoides	Poaceae	Poales	C_3	[12,13]	TRY
Vulpia octoflora	Poaceae	Poales	C_3	[10]	TRY
Whiteochloa capillipes	Poaceae	Poales	C_4	[6]	TRY
Xanthium orientale	Asteraceae	Asterales	C_3	[16]	TRY
Xanthium strumarium	Asteraceae	Asterales	C_3	[81]	N.A.
				[10,16,26]	TRY
Zea mays	Poaceae	Poales	C_4	[16,77]	TRY
Zingeria biebersteiniana	Poaceae	Poales	C_3	[6]	TRY
Zornia glochidiata	Fabaceae	Fabales	C_3	[67]	TRY

(c) Mass-based leaf N concentration

Species	Family	Order	Type	Reference	Database
Abelmoschus esculentus	Malvaceae	Malvales	C_3	[90]	N.A.
				This study	N.A.
Abutilon theophrasti	Malvaceae	Malvales	C_3	[2,91]	TRY
				[90]	N.A.
Acalypha virginica	Euphorbiaceae	Malpighiales	C_3	[3,91]	TRY
				[90]	N.A.
Aconitum gymnandrum	Ranunculaceae	Ranunculales	C_3	[4,5]	BIEN
Adonis dentata	Ranunculaceae	Ranunculales	C_3	[90]	N.A.
				[92]	TRY
Aegilops cylindrica	Poaceae	Poales	C_3	[91]	TRY
				[90]	N.A.
Aegilops geniculata	Poaceae	Poales	C_3	[2]	TRY
				[90]	N.A.
Aegilops neglecta	Poaceae	Poales	C_3	[1,93]	TRY
				[90]	N.A.
Aegilops speltoides	Poaceae	Poales	C_3	[94]	N.A.
Aegilops triuncialis	Poaceae	Poales	C_3	[95]	TRY
				[7]	BIEN
Aeluropus littoralis	Poaceae	Poales	C_4	[4]	BIEN
				[92]	TRY
Agriophyllum squarrosum	Amaranthaceae	Caryophyllales	C_4	[22,96]	TRY
Agrostemma githago	Caryophyllaceae	Caryophyllales	C_3	[90]	N.A.
Agrostis pourretii	Poaceae	Poales	C_3	[93]	TRY
				[90]	N.A.
Agrostis scabra	Poaceae	Poales	C_3	[2,97]	TRY
				[98]	BIEN
				[90]	N.A.
Aira caryophyllea	Poaceae	Poales	C_3	[90]	N.A.

				[7]	BIEN
Alloteropsis cimicina	Poaceae	Poales	C_4	[94]	N.A.
Alopecurus carolinianus	Poaceae	Poales	C_3	[91]	TRY
				[90]	N.A.
Alopecurus utriculatus	Poaceae	Poales	C_3	[93]	TRY
				[90]	N.A.
Alysicarpus schomburgkii	Fabaceae	Fabales	C_3	[99]	AusTraits
Amaranthus blitoides	Amaranthaceae	Caryophyllales	C_4	[2]	TRY
				[90]	N.A.
Amaranthus cruentus	Amaranthaceae	Caryophyllales	C_4	[90]	N.A.
				This study	N.A.
Amaranthus deflexus	Amaranthaceae	Caryophyllales	C_4	[90]	N.A.
Amaranthus hybridus	Amaranthaceae	Caryophyllales	C_4	[90,100]	N.A.
Amaranthus powellii	Amaranthaceae	Caryophyllales	C_4	[90]	N.A.
Amaranthus retroflexus	Amaranthaceae	Caryophyllales	C_4	[4]	BIEN
				[1,2]	TRY
				[90]	N.A.
Amaranthus tricolor	Amaranthaceae	Caryophyllales	C_4	[90]	N.A.
Amaranthus tuberculatus	Amaranthaceae	Caryophyllales	C_4	[91]	TRY
Amsinckia douglasiana	Boraginaceae	Boraginales	C_3	[95]	TRY
Anagallis arvensis	Primulaceae	Ericales	C_3	[90]	N.A.
Androsace septentrionalis	Primulaceae	Ericales	C_3	[101]	TRY
				[90]	N.A.
Anthemis arvensis	Asteraceae	Asterales	C_3	[93]	TRY
				[90]	N.A.
Anthemis cotula	Asteraceae	Asterales	C_3	[90]	N.A.
Anthyllis vulneraria	Fabaceae	Fabales	C_3	[102–105]	TRY
				[90]	N.A.
Aphanes arvensis	Rosaceae	Rosales	C_3	[90]	N.A.
Arabidopsis thaliana	Brassicaceae	Brassicales	C_3	[14,15,92]	TRY
				[98]	BIEN

Arachis hypogaea	Fabaceae	Fabales	C_3	18,21,90	N.A.
				4	BIEN
				92,105	TRY
				90	N.A.
				This study	N.A.
Arachis monticola	Fabaceae	Fabales	C_3	90,100	N.A.
				This study	N.A.
Arctotheca calendula	Asteraceae	Asterales	C_3	106	AusTraits
Arenaria serpyllifolia	Caryophyllaceae	Caryophyllales	C_3	90	N.A.
				107	TRY
Argemone polyanthemos	Papaveraceae	Ranunculales	C_3	91	TRY
				90	N.A.
Aristida funiculata	Poaceae	Poales	C_4	94	N.A.
Aristida oligantha	Poaceae	Poales	C_4	91	TRY
				90	N.A.
Artemisia apiacea	Asteraceae	Asterales	C_3	4	BIEN
				92	TRY
Artemisia scoparia	Asteraceae	Asterales	C_3	4,108	BIEN
				22,92,96,107	TRY
Aster subulatus	Asteraceae	Asterales	C_3	91	TRY
Astragalus pelecinus	Fabaceae	Fabales	C_3	93	TRY
				90	N.A.
Atriplex hortensis	Amaranthaceae	Caryophyllales	C_4	16	TRY
Atriplex laevis	Amaranthaceae	Caryophyllales	C_4	92	TRY
				4	BIEN
Atriplex littoralis	Amaranthaceae	Caryophyllales	C_4	90	N.A.
Atriplex patens	Amaranthaceae	Caryophyllales	C_3	4	BIEN
Atriplex sibirica	Amaranthaceae	Caryophyllales	C_4	4	BIEN
				92	TRY
Avena barbata	Poaceae	Poales	C_3	1,93,109	TRY
				106	AusTraits

				90	N.A.
				7	BIEN
Avena fatua	Poaceae	Poales	C_3	22	TRY
				4,7,98	BIEN
				90,94	N.A.
Avena sativa	Poaceae	Poales	C_3	90,94	N.A.
				110,111	TRY
				This study	N.A.
				7	BIEN
Avena sterilis	Poaceae	Poales	C_3	90,100	N.A.
				93	TRY
				This study	N.A.
Avena strigosa	Poaceae	Poales	C_3	90	N.A.
				111	TRY
Axyris amaranthoides	Amaranthaceae	Caryophyllales	C_4	22,23,112	TRY
Beta vulgaris	Amaranthaceae	Caryophyllales	C_3	90,100	N.A.
				2	TRY
Bidens bipinnata	Asteraceae	Asterales	C_3	91	TRY
				90	N.A.
				99	AusTraits
Bidens cernua	Asteraceae	Asterales	C_3	90	N.A.
				26	TRY
Bidens frondosa	Asteraceae	Asterales	C_3	90	N.A.
				26	TRY
Bidens tinctoria	Asteraceae	Asterales	C_3	101	TRY
				90	N.A.
Bidens tripartita	Asteraceae	Asterales	C_3	90	N.A.
Borago officinalis	Boraginaceae	Boraginales	C_3	90	N.A.
				This study	N.A.
Bouteloua aristidoides	Poaceae	Poales	C_4	95	TRY
Brachiaria deflexa	Poaceae	Poales	C_4	97	TRY

Brachiaria gilesii	Poaceae	Poales	C_4	113	AusTraits
Brachiaria lata	Poaceae	Poales	C_4	94	N.A.
Brachiaria plantaginea	Poaceae	Poales	C_4	97	TRY
Brachiaria pubigera	Poaceae	Poales	C_4	97,114	TRY
Brachyachne convergens	Poaceae	Poales	C_4	115	AusTraits
Brachypodium distachyon	Poaceae	Poales	C_3	1,2,93	TRY
				90	N.A.
Brachyscome iberidifolia	Asteraceae	Asterales	C_3	Firn 2019	AusTraits
Brassica carinata	Brassicaceae	Brassicales	C_3	90	N.A.
				111	TRY
Brassica juncea	Brassicaceae	Brassicales	C_3	90	N.A.
				111	TRY
Brassica napus	Brassicaceae	Brassicales	C_3	28,31,90	N.A.
				111	TRY
Brassica oleracea	Brassicaceae	Brassicales	C_3	90,100	N.A.
				This study	N.A.
Brassica rapa	Brassicaceae	Brassicales	C_3	90	N.A.
				111	TRY
Brassica tournefortii	Brassicaceae	Brassicales	C_3	90	N.A.
Briza maxima	Poaceae	Poales	C_3	33	AusTraits
				92,105	TRY
				90,94	N.A.
				7	BIEN
Bromus carinatus	Poaceae	Poales	C_3	7	BIEN
Bromus diandrus	Poaceae	Poales	C_3	7	BIEN
Bromus hordeaceus	Poaceae	Poales	C_3	1,71,93,95,97,114	TRY
				7,98	BIEN
				90	N.A.
Bromus lanceolatus	Poaceae	Poales	C_3	1,2,93	TRY
				90	N.A.
Bromus madritensis	Poaceae	Poales	C_3	1,93,95,107,109	TRY

				[90]	N.A.
Bromus pumilio	Poaceae	Poales	C_3	[94]	N.A.
Bromus rigidus	Poaceae	Poales	C_3	[90]	N.A.
Bromus rubens	Poaceae	Poales	C_3	[106]	AusTraits
Bromus sterilis	Poaceae	Poales	C_3	[92,93]	TRY
				[90]	N.A.
Bromus tectorum	Poaceae	Poales	C_3	[91,93,101]	TRY
				[90]	N.A.
Buglossoides arvensis	Boraginaceae	Boraginales	C_3	[90]	N.A.
Calystegia sepium	Convolvulaceae	Solanales	C_3	[90]	N.A.
Calystegia soldanella	Convolvulaceae	Solanales	C_3	[90]	N.A.
Calystegia sylvatica	Convolvulaceae	Solanales	C_3	[90]	N.A.
Camelina microcarpa	Brassicaceae	Brassicales	C_3	[91]	TRY
				[90]	N.A.
Camelina sativa	Brassicaceae	Brassicales	C_3	[90]	N.A.
				[111]	TRY
Campanula americana	Campanulaceae	Asterales	C_3	[91,116]	TRY
Capsicum annuum	Solanaceae	Solanales	C_3	[90,100,117]	N.A.
Carduus pycnocephalus	Asteraceae	Asterales	C_3	[92,105,118]	TRY
				[90]	N.A.
Carthamus glaucus	Asteraceae	Asterales	C_3	[93]	TRY
				[90]	N.A.
Carthamus persicus	Asteraceae	Asterales	C_3	[90]	N.A.
Carthamus tinctorius	Asteraceae	Asterales	C_3	[90]	N.A.
Catapodium rigidum	Poaceae	Poales	C_3	[1,92]	TRY
				[90]	N.A.
Cenchrus brownii	Poaceae	Poales	C_4	[94]	N.A.
Cenchrus echinatus	Poaceae	Poales	C_4	[94]	N.A.
Cenchrus longispinus	Poaceae	Poales	C_3	[91]	TRY
Cenchrus pilosus	Poaceae	Poales	C_4	[94]	N.A.
Centaurea cyanus	Asteraceae	Asterales	C_3	[3,116]	TRY

				[90]	N.A.
Centaurea solstitialis	Asteraceae	Asterales	C_3	[118]	TRY
Cerastium glomeratum	Caryophyllaceae	Caryophyllales	C_3	[93]	TRY
				[90]	N.A.
Cerastium semidecandrum	Caryophyllaceae	Caryophyllales	C_3	[90]	N.A.
Chaerophyllum procumbens	Apiaceae	Apiales	C_3	[91]	TRY
Chamaecrista fasciculata	Fabaceae	Fabales	C_3	[91]	TRY
				[90]	N.A.
Chamaecrista mimosoides	Fabaceae	Fabales	C_3	[97]	TRY
Chenopodiastrum murale	Amaranthaceae	Caryophyllales	C_3	[90]	N.A.
Chenopodiastrum simplex	Amaranthaceae	Caryophyllales	C_3	[91]	TRY
Chenopodium acuminatum	Amaranthaceae	Caryophyllales	C_3	[4]	BIEN
				[22,92,96]	TRY
Chenopodium fremontii	Amaranthaceae	Caryophyllales	C_3	[101]	TRY
				[90]	N.A.
Chenopodium hircinum	Amaranthaceae	Caryophyllales	C_3	[90]	N.A.
Chenopodium vulvaria	Amaranthaceae	Caryophyllales	C_3	[22,96,101]	TRY
				[90]	N.A.
Chloris virgata	Poaceae	Poales	C_4	[22,92,96,97]	TRY
				[4]	BIEN
				[90]	N.A.
Chylismia brevipes	Onagraceae	Myrtales	C_3	[2]	TRY
Chylismia claviformis	Onagraceae	Myrtales	C_3	[2]	TRY
Cicer arietinum	Fabaceae	Fabales	C_3	[90]	N.A.
Cicer reticulatum	Fabaceae	Fabales	C_3	[90]	N.A.
Citrullus lanatus	Cucurbitaceae	Cucurbitales	C_3	[90]	N.A.
Cladanthus mixtus	Asteraceae	Asterales	C_3	[93]	TRY
Coix lacryma-jobi	Poaceae	Poales	C_4	[94]	N.A.
Coldenia procumbens	Boraginaceae	Boraginales	C_3	[99]	AusTraits
Commelina communis	Commelinaceae	Commelinales	C_3	[4]	BIEN
				[92]	TRY

Conium maculatum	Apiaceae	Apiales	C_3	91	TRY
				90	N.A.
Conobea multifida	Plantaginaceae	Lamiales	C_3	91	TRY
Corchorus aestuans	Malvaceae	Malvales	C_3	90	N.A.
Corispermum heptapotamicum	Amaranthaceae	Caryophyllales	C_4	22	TRY
Corispermum hyssopifolium	Amaranthaceae	Caryophyllales	C_3	4	BIEN
				92	TRY
Corispermum mongolicum	Amaranthaceae	Caryophyllales	C_3	22	TRY
Corispermum orientale	Amaranthaceae	Caryophyllales	C_3	4	BIEN
				92	TRY
Cosmos parviflorus	Asteraceae	Asterales	C_3	101	TRY
				90	N.A.
Crassocephalum crepidioides	Asteraceae	Asterales	C_3	22	TRY
Crepis biennis	Asteraceae	Asterales	C_3	71,93	TRY
				90	N.A.
Crepis capillaris	Asteraceae	Asterales	C_3	90	N.A.
Crepis foetida	Asteraceae	Asterales	C_3	93,95,107,109	TRY
				90	N.A.
Crepis nicaeensis	Asteraceae	Asterales	C_3	96	TRY
Crepis sancta	Asteraceae	Asterales	C_3	93	TRY
				90	N.A.
Crepis vesicaria	Asteraceae	Asterales	C_3	90	N.A.
Croton capitatus	Euphorbiaceae	Malpighiales	C_3	91	TRY
				90	N.A.
Croton monanthogynus	Euphorbiaceae	Malpighiales	C_3	91	TRY
Cucumis sativus	Cucurbitaceae	Cucurbitales	C_3	90	N.A.
Cutandia dichotoma	Poaceae	Poales	C_3	92	TRY
Cynosurus echinatus	Poaceae	Poales	C_3	7	BIEN
Cyperus acuminatus	Cyperaceae	Poales	C_3	91	TRY
				90	N.A.
Cyperus aquatilis	Cyperaceae	Poales	C_3	99	AusTraits

Cyperus diandrus	Cyperaceae	Poales	C_4	26	TRY
Cyperus flavidus	Cyperaceae	Poales	C_4	90	N.A.
				37	TRY
Cyperus reduncus	Cyperaceae	Poales	C_4	26	TRY
Dactyloctenium aegyptium	Poaceae	Poales	C_4	97	TRY
				90,94	N.A.
Dactyloctenium giganteum	Poaceae	Poales	C_4	94	N.A.
Dactyloctenium radulans	Poaceae	Poales	C_4	93	AusTraits
				94	N.A.
Dalea polygonoides	Fabaceae	Fabales	C_3	101	TRY
				90	N.A.
Danthoniopsis dinteri	Poaceae	Poales	C_4	94	N.A.
Dasypyrum villosum	Poaceae	Poales	C_3	94	N.A.
Delphinium consolida	Ranunculaceae	Ranunculales	C_3	90	N.A.
Descurainia sophia	Brassicaceae	Brassicales	C_3	4	BIEN
				90	N.A.
				92	TRY
Descurainia titicacensis	Brassicaceae	Brassicales	C_3	105	TRY
Desmodium brownii	Fabaceae	Fabales	C_3	99	AusTraits
Diarthron linifolium	Thymelaeaceae	Malvales	C_3	4	BIEN
Digitaria bicornis	Poaceae	Poales	C_4	97,114	TRY
Digitaria ciliaris	Poaceae	Poales	C_4	94	N.A.
Digitaria ischaemum	Poaceae	Poales	C_4	90	N.A.
				3,26	TRY
Digitaria sanguinalis	Poaceae	Poales	C_4	91,97,119	TRY
				90,94	N.A.
Digitaria setigera	Poaceae	Poales	C_4	94	N.A.
Digitaria velutina	Poaceae	Poales	C_4	97	TRY
Diheteropogon hagerupii	Poaceae	Poales	C_4	94	N.A.
Dontostemon micranthus	Brassicaceae	Brassicales	C_3	23	TRY
				108	BIEN

Dracocephalum moldavica	Lamiaceae	Lamiales	C_3	120	BIEN
Dysphania aristata	Amaranthaceae	Caryophyllales	C_3	22,96	TRY
Dysphania kalpari	Amaranthaceae	Caryophyllales	C_3	113	AusTraits
Echinochloa cruspavonis	Poaceae	Poales	C_4	94	N.A.
Echinochloa frumentacea	Poaceae	Poales	C_4	90,94	N.A.
Echinochloa muricata	Poaceae	Poales	C_4	91	TRY
				94	N.A.
Echinochloa oryzoides	Poaceae	Poales	C_4	94	N.A.
Echinochloa stagnina	Poaceae	Poales	C_4	94	N.A.
Echium plantagineum	Boraginaceae	Boraginales	C_3	90	N.A.
				16,93	TRY
Ectrosia leporina	Poaceae	Poales	C_4	99	AusTraits
Eleocharis obtusa	Cyperaceae	Poales	C_3	90	N.A.
				26	TRY
Eleusine coracana	Poaceae	Poales	C_4	94	N.A.
Eleusine indica	Poaceae	Poales	C_4	91	TRY
				90,94	N.A.
Ellisia nyctelea	Boraginaceae	Boraginales	C_3	91	TRY
Enneapogon polyphyllus	Poaceae	Poales	C_4	97,114	TRY
				113	AusTraits
				90	N.A.
Enteropogon prieurii	Poaceae	Poales	C_4	94	N.A.
Epaltes australis	Asteraceae	Asterales	C_3	106	AusTraits
Eragrostis cilianensis	Poaceae	Poales	C_4	90,94	N.A.
				22,91,96	TRY
				4	BIEN
Eragrostis cummingii	Poaceae	Poales	C_4	97,114	TRY
Eragrostis mexicana	Poaceae	Poales	C_4	101	TRY
				90,94	N.A.
Eragrostis minor	Poaceae	Poales	C_4	22,96	TRY
				90	N.A.

				[4]	BIEN
Eragrostis pectinacea	Poaceae	Poales	C_4	[90,94]	N.A.
				[26,91]	TRY
Eragrostis pilosa	Poaceae	Poales	C_4	[90,94]	N.A.
Eragrostis tef	Poaceae	Poales	C_4	[90]	N.A.
Eragrostis unioloides	Poaceae	Poales	C_4	[94]	N.A.
Eremopyrum triticeum	Poaceae	Poales	C_3	[92]	TRY
				[94]	N.A.
Eriachne aristidea	Poaceae	Poales	C_4	[97,114]	TRY
				[94]	N.A.
Eriachne avenacea	Poaceae	Poales	C_4	[99]	AusTraits
Eriachne burkittii	Poaceae	Poales	C_4	[99]	AusTraits
Eriachne ciliata	Poaceae	Poales	C_4	[97,114]	TRY
Erigeron annuus	Asteraceae	Asterales	C_3	[91]	TRY
				[90]	N.A.
Erigeron floribundus	Asteraceae	Asterales	C_3	[93,95,109]	TRY
				[90]	N.A.
Erigeron philadelphicus	Asteraceae	Asterales	C_3	[91]	TRY
				[90]	N.A.
Erigeron strigosus	Asteraceae	Asterales	C_3	[91]	TRY
				[90]	N.A.
Eriochloa contracta	Poaceae	Poales	C_3	[91]	TRY
Eriogonum pharnaceoides	Polygonaceae	Caryophyllales	C_3	[101]	TRY
				[90]	N.A.
Erodium botrys	Geraniaceae	Geraniales	C_3	[95,105]	TRY
				[106]	AusTraits
				[90]	N.A.
Erodium ciconium	Geraniaceae	Geraniales	C_3	[93]	TRY
				[90]	N.A.
Eruca vesicaria	Brassicaceae	Brassicales	C_3	[90]	N.A.
				[111,121]	TRY

Erythranthe glabrata	Phrymaceae	Lamiales	C_3	91	TRY
Euclidium syriacum	Brassicaceae	Brassicales	C_3	92	TRY
Euphorbia falcata	Euphorbiaceae	Malpighiales	C_3	90	N.A.
Euphorbia glyptosperma	Euphorbiaceae	Malpighiales	C_4	91	TRY
Euphorbia helioscopia	Euphorbiaceae	Malpighiales	C_3	90	N.A.
				92,105	TRY
Euphorbia humifusa	Euphorbiaceae	Malpighiales	C_4	22	TRY
Euphorbia maculata	Euphorbiaceae	Malpighiales	C_4	91	TRY
				90	N.A.
Euphorbia missurica	Euphorbiaceae	Malpighiales	C_4	91	TRY
Euphorbia nutans	Euphorbiaceae	Malpighiales	C_4	91	TRY
				90	N.A.
Euphorbia peplus	Euphorbiaceae	Malpighiales	C_4	90	N.A.
Euphorbia serpyllifolia	Euphorbiaceae	Malpighiales	C_4	101	TRY
				90	N.A.
Euphorbia spathulata	Euphorbiaceae	Malpighiales	C_3	91	TRY
				90	N.A.
Fagopyrum esculentum	Polygonaceae	Caryophyllales	C_3	90	N.A.
				111	TRY
Fagopyrum homotropicum	Polygonaceae	Caryophyllales	C_3	90	N.A.
Filago desertorum	Asteraceae	Asterales	C_3	121	TRY
				90	N.A.
Filago gallica	Asteraceae	Asterales	C_3	93	TRY
				90	N.A.
Galactites tomentosa	Asteraceae	Asterales	C_3	93	TRY
Galeopsis ladanum	Lamiaceae	Lamiales	C_3	105	TRY
				90	N.A.
Galeopsis segetum	Lamiaceae	Lamiales	C_3	90	N.A.
Galeopsis speciosa	Lamiaceae	Lamiales	C_3	105,122	TRY
				90	N.A.
Gentiana parvula	Gentianaceae	Gentianales	C_3	123	BIEN

Gentianella amarella	Gentianaceae	Gentianales	C_3	90	N.A.
				75,92	TRY
Gentianopsis paludosa	Gentianaceae	Gentianales	C_3	123	BIEN
Geranium carolinianum	Geraniaceae	Geraniales	C_3	91	TRY
			C_3	90	N.A.
Glycine max	Fabaceae	Fabales	C_3	4	BIEN
				90	N.A.
				1,77	TRY
Gnaphalium affine	Asteraceae	Asterales	C_3	2	TRY
				4	BIEN
Gnaphalium luteoalbum	Asteraceae	Asterales	C_3	5	BIEN
				90	N.A.
Grubovia dasyphylla	Amaranthaceae	Caryophyllales	C_4	22,96	TRY
Guizotia abyssinica	Asteraceae	Asterales	C_3	90	N.A.
				111	TRY
Gutierrezia dracunculoides	Asteraceae	Asterales	C_3	91	TRY
Halenia elliptica	Gentianaceae	Gentianales	C_3	123	BIEN
Hedeoma hispida	Lamiaceae	Lamiales	C_3	91	TRY
				90	N.A.
Helianthus agrestis	Asteraceae	Asterales	C_3	39	BIEN
Helianthus annuus	Asteraceae	Asterales	C_3	1,91,97,107,111	TRY
				90,100	N.A.
				39	BIEN
Helianthus argophyllus	Asteraceae	Asterales	C_3	39	BIEN
Helianthus debilis	Asteraceae	Asterales	C_3	39	BIEN
				90	N.A.
Helianthus neglectus	Asteraceae	Asterales	C_3	39	BIEN
Helianthus praecox	Asteraceae	Asterales	C_3	39	BIEN
Hibiscus trionum	Malvaceae	Malvales	C_3	91,92	TRY
			C_3	4	BIEN
			C_3	90	N.A.

Hordeum murinum	Poaceae	Poales	C_3	[1]	TRY
				[98]	BIEN
				[90]	N.A.
Hordeum pusillum	Poaceae	Poales	C_3	[91]	TRY
				[90]	N.A.
Hordeum spontaneum	Poaceae	Poales	C_3	[94,100]	N.A.
Hordeum vulgare	Poaceae	Poales	C_3	[90,94]	N.A.
Hyparrhenia confinis	Poaceae	Poales	C_4	[97]	TRY
Hypecoum leptocarpum	Papaveraceae	Ranunculales	C_3	[123]	BIEN
Hypericum gramineum	Hypericaceae	Malpighiales	C_3	[124]	AusTraits
Hypochaeris glabra	Asteraceae	Asterales	C_3	[90]	N.A.
Ifloga spicata	Asteraceae	Asterales	C_3	[90]	N.A.
				[92]	TRY
Impatiens balfourii	Balsaminaceae	Ericales	C_3	[90]	N.A.
Impatiens capensis	Balsaminaceae	Ericales	C_3	[90]	N.A.
				[37,92]	TRY
Impatiens furcillata	Balsaminaceae	Ericales	C_3	[22,96]	TRY
Impatiens noli-tangere	Balsaminaceae	Ericales	C_3	[90]	N.A.
Impatiens pallida	Balsaminaceae	Ericales	C_3	[90]	N.A.
				[92]	TRY
Impatiens rubrostriata	Balsaminaceae	Ericales	C_3	[22]	TRY
Incarvillea sinensis	Bignoniaceae	Lamiales	C_3	[120]	BIEN
Ischaemum rugosum	Poaceae	Poales	C_4	[94]	N.A.
Iseilema membranaceum	Poaceae	Poales	C_4	[125]	AusTraits
Iva annua	Asteraceae	Asterales	C_3	[91]	TRY
Ixeridium gracile	Asteraceae	Asterales	C_3	[22]	TRY
Ixeris chinensis	Asteraceae	Asterales	C_3	[96]	TRY
Ixeris polycephala	Asteraceae	Asterales	C_3	[120]	BIEN
Jacobaea vulgaris	Asteraceae	Asterales	C_3	[93,105]	TRY
				[90]	N.A.
Kali collinum	Amaranthaceae	Caryophyllales	C_4	[22,23,92,96]	TRY

			C_4	4,120,126	BIEN
Kalimeris altaica	Asteraceae	Asterales	C_3	4,120	BIEN
				22,92,96	TRY
Kickxia spuria	Plantaginaceae	Lamiales	C_3	90	N.A.
Koelpinia linearis	Asteraceae	Asterales	C_3	121	TRY
				90	N.A.
Krigia caespitosa	Asteraceae	Asterales	C_3	91	TRY
Kummerowia striata	Fabaceae	Fabales	C_3	90	N.A.
				22,96	TRY
Lactuca canadensis	Asteraceae	Asterales	C_3	91	TRY
Lactuca ludoviciana	Asteraceae	Asterales	C_3	91	TRY
Lactuca saligna	Asteraceae	Asterales	C_3	91	TRY
				90	N.A.
Lactuca sativa	Asteraceae	Asterales	C_3	90	N.A.
				This study	N.A.
Lactuca serriola	Asteraceae	Asterales	C_3	91	TRY
				90,100	N.A.
				98	BIEN
				This study	N.A.
Laennecia schiedeana	Asteraceae	Asterales	C_3	101	TRY
				90	N.A.
Lagurus ovatus	Poaceae	Poales	C_3	92,105	TRY
				90	N.A.
Lamium amplexicaule	Lamiaceae	Lamiales	C_3	90	N.A.
Lamium purpureum	Lamiaceae	Lamiales	C_3	90	N.A.
Laportea canadensis	Urticaceae	Rosales	C_3	91,92	TRY
Lappula marginata	Boraginaceae	Boraginales	C_3	92	TRY
				4	BIEN
Lappula semiglabra	Boraginaceae	Boraginales	C_3	4	BIEN
Lapsana communis	Asteraceae	Asterales	C_3	90	N.A.
Lapsanastrum humile	Asteraceae	Asterales	C_3	127	TRY

Lathyrus cicera	Fabaceae	Fabales	C_3	90	N.A.
Lathyrus hirsutus	Fabaceae	Fabales	C_3	90	N.A.
Lathyrus sativus	Fabaceae	Fabales	C_3	90	N.A.
				111	TRY
Legousia speculum-veneris	Campanulaceae	Asterales	C_3	90	N.A.
Lens culinaris	Fabaceae	Fabales	C_3	90	N.A.
Leonurus sibiricus	Lamiaceae	Lamiales	C_3	4	BIEN
				92	TRY
Lepidium densiflorum	Brassicaceae	Brassicales	C_3	91,97,101	TRY
				90	N.A.
Lepidium ruderale	Brassicaceae	Brassicales	C_3	90	N.A.
Lepidium sativum	Brassicaceae	Brassicales	C_3	90	N.A.
Leptochloa fusca	Poaceae	Poales	C_4	91,97,114	TRY
				90	N.A.
Leptochloa panicoides	Poaceae	Poales	C_4	94	N.A.
Leptochloa virgata	Poaceae	Poales	C_4	94	N.A.
Linaria supina	Plantaginaceae	Lamiales	C_3	128	TRY
				90	N.A.
Lindernia dubia	Linderniaceae	Lamiales	C_3	90	N.A.
Linum australe	Linaceae	Malpighiales	C_3	101	TRY
				90	N.A.
Linum stelleroides	Linaceae	Malpighiales	C_3	120	BIEN
Linum sulcatum	Linaceae	Malpighiales	C_3	91	TRY
Linum usitatissimum	Linaceae	Malpighiales	C_3	93	TRY
				90	N.A.
Lipandra polysperma	Amaranthaceae	Caryophyllales	C_3	3,26,116	TRY
				90	N.A.
Lolium rigidum	Poaceae	Poales	C_3	1,93	TRY
				90	N.A.
Lolium X	Poaceae	Poales	C_3	90	N.A.
				111	TRY

Lotus angustissimus	Fabaceae	Fabales	C_3	93	TRY
				90	N.A.
Lotus corniculatus	Fabaceae	Fabales	C_3	11,71,92,93,95,104,105,128–132	TRY
				98	BIEN
				90	N.A.
Loudetiopsis kerstingii	Poaceae	Poales	C_4	94	N.A.
Luffa acutangula	Cucurbitaceae	Cucurbitales	C_3	90	N.A.
Luffa aegyptiaca	Cucurbitaceae	Cucurbitales	C_3	99	AusTraits
Lupinus bicolor	Fabaceae	Fabales	C_3	95	TRY
				98	BIEN
				90	N.A.
Lupinus kingii	Fabaceae	Fabales	C_3	101	TRY
				90	N.A.
Malvastrum hispidum	Malvaceae	Malvales	C_3	91	TRY
Medicago orbicularis	Fabaceae	Fabales	C_3	92,105	TRY
				90	N.A.
Medicago polyceratia	Fabaceae	Fabales	C_3	121	TRY
Melinis repens	Poaceae	Poales	C_4	97	TRY
				90,94	N.A.
Mentha spicata	Lamiaceae	Lamiales	C_3	90	N.A.
Mercurialis annua	Euphorbiaceae	Malpighiales	C_3	90	N.A.
Microstegium vimineum	Poaceae	Poales	C_4	37	TRY
Mitreola sessilifolia	Loganiaceae	Gentianales	C_3	92	TRY
Moehringia trinervia	Caryophyllaceae	Caryophyllales	C_3	90	N.A.
Mollugo verticillata	Molluginaceae	Caryophyllales	C_4	91,97	TRY
Mosla dianthera	Lamiaceae	Lamiales	C_3	4	BIEN
				92	TRY
Muhlenbergia minutissima	Poaceae	Poales	C_4	101	TRY
				90	N.A.
Muhlenbergia peruviana	Poaceae	Poales	C_4	95	TRY
Muhlenbergia ramulosa	Poaceae	Poales	C_4	101	TRY

				[90]	N.A.
Munroa squarrosa	Poaceae	Poales	C_4	[90]	N.A.
Myagrum perfoliatum	Brassicaceae	Brassicales	C_3	[116]	TRY
Myosotis verna	Boraginaceae	Boraginales	C_3	[91]	TRY
Nama dichotoma	Boraginaceae	Boraginales	C_3	[101]	TRY
Nigella damascena	Ranunculaceae	Ranunculales	C_3	[116]	TRY
Nigella sativa	Ranunculaceae	Ranunculales	C_3	[90]	N.A.
Notoceras bicorne	Brassicaceae	Brassicales	C_3	[121]	TRY
				[90]	N.A.
Nototriche pusilla	Malvaceae	Malvales	C_3	[105]	TRY
Oenothera curtiflora	Onagraceae	Myrtales	C_3	[91]	TRY
Oenothera filiformis	Onagraceae	Myrtales	C_3	[91]	TRY
Oenothera nana	Onagraceae	Myrtales	C_3	[105]	TRY
Orlaya grandiflora	Apiaceae	Apiales	C_3	[93]	TRY
				[90]	N.A.
Ornithopus compressus	Fabaceae	Fabales	C_3	[93,110]	TRY
				[90]	N.A.
Ornithopus perpusillus	Fabaceae	Fabales	C_3	[90]	N.A.
Oryza barthii	Poaceae	Poales	C_3	[94]	N.A.
Oryza eichingeri	Poaceae	Poales	C_3	[94]	N.A.
Oryza glaberrima	Poaceae	Poales	C_3	[94]	N.A.
Oryza grandiglumis	Poaceae	Poales	C_3	[94]	N.A.
Oryza latifolia	Poaceae	Poales	C_3	[41]	N.A.
Oryza punctata	Poaceae	Poales	C_3	[41,90]	N.A.
Oryza rufipogon	Poaceae	Poales	C_3	[41,90]	N.A.
				[16]	TRY
Oryza sativa	Poaceae	Poales	C_3	[41,43,49–51,53,90]	N.A.
				[4]	BIEN
				[1,16,92,105]	TRY
Oxybasis glauca	Amaranthaceae	Caryophyllales	C_4	[22,23,92,96,112]	TRY
				[4]	BIEN

				90	N.A.
Oxychloris scariosa	Poaceae	Poales	C_4	94	N.A.
Panicum bisulcatum	Poaceae	Poales	C_3	94	N.A.
Panicum capillare	Poaceae	Poales	C_4	2,3,26,91	TRY
				90	N.A.
Panicum dichotomiflorum	Poaceae	Poales	C_4	91	TRY
				90,94	N.A.
Panicum flexuosum	Poaceae	Poales	C_4	94	N.A.
				22	TRY
Panicum laetum	Poaceae	Poales	C_4	94	N.A.
Panicum miliaceum	Poaceae	Poales	C_4	90,94	N.A.
Panicum trichoides	Poaceae	Poales	C_3	97	TRY
				90	N.A.
Papaver rhoeas	Papaveraceae	Ranunculales	C_3	90	N.A.
Papaver somniferum	Papaveraceae	Ranunculales	C_3	90	N.A.
Parahyparrhenia annua	Poaceae	Poales	C_4	111	TRY
Parakeelya corrigioloides	Montiaceae	Caryophyllales	C_3	92	TRY
Parietaria pensylvanica	Urticaceae	Rosales	C_3	91	TRY
				90	N.A.
Paronychia arabica	Caryophyllaceae	Caryophyllales	C_3	121	TRY
Paspalidium clementei	Poaceae	Poales	C_4	125	AusTraits
Pelargonium columbinum	Geraniaceae	Geraniales	C_3	97	TRY
Pelargonium senecioides	Geraniaceae	Geraniales	C_3	97	TRY
Pennisetum basedowii	Poaceae	Poales	C_4	115	AusTraits
Pennisetum glaucum	Poaceae	Poales	C_4	90,100	N.A.
				4	BIEN
				3,92	TRY
				This study	N.A.
Pennisetum sieberianum	Poaceae	Poales	C_4	94	N.A.
Pennisetum violaceum	Poaceae	Poales	C_4	94	N.A.
Pentameris airoides	Poaceae	Poales	C_3	106	AusTraits

Perotis patens	Poaceae	Poales	C_4	114	TRY
				90	N.A.
Persicaria bungeana	Polygonaceae	Caryophyllales	C_3	2,26,91	TRY
Persicaria lapathifolia	Polygonaceae	Caryophyllales	C_3	90	N.A.
				26	TRY
Persicaria maculosa	Polygonaceae	Caryophyllales	C_3	91	TRY
				90	N.A.
Persicaria mitis	Polygonaceae	Caryophyllales	C_3	90	N.A.
Persicaria sagittata	Polygonaceae	Caryophyllales	C_3	90	N.A.
Phalaris paradoxa	Poaceae	Poales	C_3	93	TRY
				90	N.A.
Phaseolus lunatus	Fabaceae	Fabales	C_3	90	N.A.
Phaseolus vulgaris	Fabaceae	Fabales	C_3	56,90	N.A.
				1,133	TRY
Phoebanthus tenuifolius	Asteraceae	Asterales	C_3	39	BIEN
Pilea pumila	Urticaceae	Rosales	C_3	91	TRY
Pimpinella cretica	Apiaceae	Apiales	C_3	93	TRY
				90	N.A.
Pisum sativum	Fabaceae	Fabales	C_3	90	N.A.
				111	TRY
Plantago argyrea	Plantaginaceae	Lamiales	C_3	101	TRY
				90	N.A.
Plantago aristata	Plantaginaceae	Lamiales	C_3	91	TRY
Plantago ciliata	Plantaginaceae	Lamiales	C_3	121	TRY
				90	N.A.
Plantago major	Plantaginaceae	Lamiales	C_3	3,15,16,26,105,122,134	TRY
				98	BIEN
				90	N.A.
Plantago minuta	Plantaginaceae	Lamiales	C_3	4	BIEN
Plantago ovata	Plantaginaceae	Lamiales	C_3	121	TRY
				90	N.A.

Plantago patagonica	Plantaginaceae	Lamiales	C_3	91	TRY
				90	N.A.
Plantago rhodosperma	Plantaginaceae	Lamiales	C_3	91	TRY
Plantago virginica	Plantaginaceae	Lamiales	C_3	91	TRY
Poa annua	Poaceae	Poales	C_3	1,16,22,57,92,93,95,129,131	TRY
				4,98	BIEN
				90	N.A.
Podolepis lessonii	Asteraceae	Asterales	C_3	106	AusTraits
Polycnemum arvense	Amaranthaceae	Caryophyllales	C_3	90	N.A.
				22,96	TRY
Polygala myrtifolia	Polygalaceae	Fabales	C_3	135	BIEN
Polygonum aviculare	Polygonaceae	Caryophyllales	C_4	22,91,92,96,101,122	TRY
				4,98	BIEN
				90	N.A.
Polygonum douglasii	Polygonaceae	Caryophyllales	C_3	90	N.A.
Polygonum ramosissimum	Polygonaceae	Caryophyllales	C_3	91	TRY
Polygonum tenue	Polygonaceae	Caryophyllales	C_3	91	TRY
Polytoca hubbardiana	Poaceae	Poales	C_4	115	AusTraits
Portulaca bicolor	Portulacaceae	Caryophyllales	C_3	99	AusTraits
Potentilla norvegica	Rosaceae	Rosales	C_3	122	TRY
				90	N.A.
Pseudognaphalium obtusifolium	Asteraceae	Asterales	C_3	91	TRY
Ptilotus aervoides	Amaranthaceae	Caryophyllales	C_3	113	AusTraits
Ptilotus macrocephalus	Amaranthaceae	Caryophyllales	C_4	113	AusTraits
Pulicaria arabica	Asteraceae	Asterales	C_3	93	TRY
				90	N.A.
Ranunculus arvensis	Ranunculaceae	Ranunculales	C_3	90	N.A.
Ranunculus sceleratus	Ranunculaceae	Ranunculales	C_3	90	N.A.
Raphanus raphanistrum	Brassicaceae	Brassicales	C_3	90	N.A.
				16,111	TRY
Rapistrum rugosum	Brassicaceae	Brassicales	C_3	93	TRY

				90	N.A.
Reseda phyteuma	Resedaceae	Brassicales	C_3	128	TRY
				90	N.A.
Rostraria cristata	Poaceae	Poales	C_3	2,3,23,92,112,114,119,136	TRY
				4,5,123	BIEN
				94	N.A.
Rudbeckia amplexicaulis	Asteraceae	Asterales	C_3	91	TRY
Rudbeckia hirta	Asteraceae	Asterales	C_3	90	N.A.
Rumex pictus	Polygonaceae	Caryophyllales	C_3	92	TRY
Salicornia europaea	Amaranthaceae	Caryophyllales	C_3	22,92,96,130,137	TRY
				4	BIEN
				90	N.A.
Schismus barbatus	Poaceae	Poales	C_3	121	TRY
				90	N.A.
Schizachyrium crinizonatum	Poaceae	Poales	C_4	114,136	TRY
Schizachyrium fragile	Poaceae	Poales	C_4	99	AusTraits
Schmidtia kalahariensis	Poaceae	Poales	C_4	136	TRY
				90	N.A.
Scolymus maculatus	Asteraceae	Asterales	C_3	93	TRY
				90	N.A.
Secale cereale	Poaceae	Poales	C_3	90,94,100	N.A.
				92,111	TRY
Sesamum indicum	Pedaliaceae	Lamiales	C_3	4	BIEN
				90	N.A.
				92	TRY
				This study	N.A.
Setaria helvola	Poaceae	Poales	C_4	91	TRY
				90	N.A.
Setaria italica	Poaceae	Poales	C_4	4	BIEN
				90,94	N.A.
				92,111	TRY

Setaria verticillata	Poaceae	Poales	C_4	94	N.A.
Setaria viridis	Poaceae	Poales	C_4	3,22,91,96	TRY
				90,94	N.A.
				4,120	BIEN
Sicyos angulatus	Cucurbitaceae	Cucurbitales	C_3	91	TRY
				90	N.A.
Sigesbeckia orientalis	Asteraceae	Asterales	C_3	58	AusTraits
Silene antirrhina	Caryophyllaceae	Caryophyllales	C_3	91	TRY
Sinapis alba	Brassicaceae	Brassicales	C_3	90	N.A.
				111	TRY
Siphonostegia chinensis	Orobanchaceae	Lamiales	C_3	120	BIEN
Solanum aethiopicum	Solanaceae	Solanales	C_3	90	N.A.
Solanum lycopersicum	Solanaceae	Solanales	C_3	90	N.A.
				This study	N.A.
Solanum pimpinellifolium	Solanaceae	Solanales	C_3	90,100	N.A.
				This study	N.A.
Solanum ptychanthum	Solanaceae	Solanales	C_3	91	TRY
Solanum rostratum	Solanaceae	Solanales	C_3	91	TRY
Sonchus asper	Asteraceae	Asterales	C_3	91	TRY
				98	BIEN
				90	N.A.
Sonchus oleraceus	Asteraceae	Asterales	C_3	106	AusTraits
				4,98,120	BIEN
				90	N.A.
				22,92,96	TRY
Sorghum amplum	Poaceae	Poales	C_4	94	N.A.
Sorghum angustum	Poaceae	Poales	C_4	94	N.A.
Sorghum arundinaceum	Poaceae	Poales	C_4	90,94	N.A.
Sorghum bicolor	Poaceae	Poales	C_4	4	BIEN
				90,94	N.A.
				92	TRY

				[138]	AusTraits
Sorghum brachypodum	Poaceae	Poales	C_4	[99]	AusTraits
Sorghum ecarinatum	Poaceae	Poales	C_4	[94]	N.A.
Sorghum intrans	Poaceae	Poales	C_4	[114,136]	TRY
Sorghum timorense	Poaceae	Poales	C_4	[115]	AusTraits
				[94]	N.A.
Spergularia diandra	Caryophyllaceae	Caryophyllales	C_3	[121]	TRY
				[90]	N.A.
Spergularia media	Caryophyllaceae	Caryophyllales	C_3	[137]	TRY
Spergularia rubra	Caryophyllaceae	Caryophyllales	C_3	[98]	BIEN
				[90]	N.A.
Sphenopholis obtusata	Poaceae	Poales	C_3	[91]	TRY
				[90]	N.A.
Spinacia oleracea	Amaranthaceae	Caryophyllales	C_3	[90]	N.A.
Spinacia turkestanica	Amaranthaceae	Caryophyllales	C_3	[90]	N.A.
Sporobolus australasicus	Poaceae	Poales	C_4	[115]	AusTraits
Sporobolus panicoides	Poaceae	Poales	C_4	[136]	TRY
				[90]	N.A.
Stellaria neglecta	Caryophyllaceae	Caryophyllales	C_3	[90]	N.A.
Stellaria pallida	Caryophyllaceae	Caryophyllales	C_3	[90]	N.A.
Stipa capensis	Poaceae	Poales	C_3	[107,121,139]	TRY
				[90,94]	N.A.
Streptoglossa cylindriceps	Asteraceae	Asterales	C_3	[124]	AusTraits
Strigosella africana	Brassicaceae	Brassicales	C_3	[92,105]	TRY
				[90]	N.A.
Suaeda glauca	Amaranthaceae	Caryophyllales	C_4	[4]	BIEN
				[22,92]	TRY
Suaeda heterophylla	Amaranthaceae	Caryophyllales	C_4	[22,96]	TRY
Suaeda salsa	Amaranthaceae	Caryophyllales	C_3	[4]	BIEN
Taeniatherum caputmedusae	Poaceae	Poales	C_3	[93,95]	TRY
				[7,98]	BIEN

				90	N.A.
Teesdalia nudicaulis	Brassicaceae	Brassicales	C_3	90	N.A.
Tetracme quadricornis	Brassicaceae	Brassicales	C_3	4	BIEN
				92	TRY
Teucrium canadense	Lamiaceae	Lamiales	C_3	91	TRY
				90	N.A.
Thlaspi arvense	Brassicaceae	Brassicales	C_3	90	N.A.
Tolpis barbata	Asteraceae	Asterales	C_3	93	TRY
				90	N.A.
Tordylium apulum	Apiaceae	Apiales	C_3	92,105	TRY
				90	N.A.
Torilis arvensis	Apiaceae	Apiales	C_3	91	TRY
				90	N.A.
Trachymene pilosa	Araliaceae	Apiales	C_3	92	TRY
Tragus berteronianus	Poaceae	Poales	C_4	1,105,140	TRY
				90	N.A.
Tragus racemosus	Poaceae	Poales	C_4	90,94	N.A.
				22,96	TRY
Tribolium echinatum	Poaceae	Poales	C_3	94	N.A.
Tribulus terrestris	Zygophyllaceae	Zygophyllales	C_4	22,91,92,96,105	TRY
				4	BIEN
				90	N.A.
Trifolium angustifolium	Fabaceae	Fabales	C_3	93,107	TRY
				90	N.A.
Trifolium arvense	Fabaceae	Fabales	C_3	106	AusTraits
				93	TRY
				90	N.A.
Trifolium bocconei	Fabaceae	Fabales	C_3	93	TRY
				90	N.A.
Trifolium campestre	Fabaceae	Fabales	C_3	71,93	TRY
				90	N.A.

Trifolium cherleri	Fabaceae	Fabales	C_3	93	TRY
				90	N.A.
Trifolium microcephalum	Fabaceae	Fabales	C_3	95	TRY
				98	BIEN
Trifolium purpureum	Fabaceae	Fabales	C_3	93	TRY
				90	N.A.
Trifolium repens	Fabaceae	Fabales	C_3	1,2,11,71,91,93,104,105,122,127,129,136,141	TRY
				98	BIEN
				90	N.A.
Trifolium stellatum	Fabaceae	Fabales	C_3	92,105	TRY
				90	N.A.
Trigonella alba	Fabaceae	Fabales	C_3	2,22,116,122	TRY
				4	BIEN
				90	N.A.
Trigonella foenum-graecum	Fabaceae	Fabales	C_3	4	BIEN
				90	N.A.
				92,111	TRY
Trigonella officinalis	Fabaceae	Fabales	C_3	3,91,92,111	TRY
				4,120	BIEN
				90	N.A.
Triodanis leptocarpa	Campanulaceae	Asterales	C_3	91	TRY
Tripleurospermum inodorum	Asteraceae	Asterales	C_4	122	TRY
Tripleurospermum maritimum	Asteraceae	Asterales	C_3	93	TRY
				90	N.A.
Triticum aestivum	Poaceae	Poales	C_3	61,64,65,90,94	N.A.
				4	BIEN
				1,66,92	TRY
Triticum dicoccoides	Poaceae	Poales	C_3	90,100	N.A.
				93	TRY
Triticum monococcum	Poaceae	Poales	C_3	90,94	N.A.
Triticum timopheevii	Poaceae	Poales	C_3	94	N.A.

Triticum turgidum	Poaceae	Poales	C_3	[66]	TRY
				[90]	N.A.
Urochloa trichopus	Poaceae	Poales	C_4	[136]	TRY
Valerianella locusta	Caprifoliaceae	Dipsacales	C_3	[90]	N.A.
Valerianella rimosa	Caprifoliaceae	Dipsacales	C_3	[90]	N.A.
Veronica arvensis	Plantaginaceae	Lamiales	C_3	[93]	TRY
				[90]	N.A.
Veronica hederifolia	Plantaginaceae	Lamiales	C_3	[90]	N.A.
Veronica persica	Plantaginaceae	Lamiales	C_3	[11,93,107]	TRY
				[90]	N.A.
Vicia faba	Fabaceae	Fabales	C_3	[90]	N.A.
				This study	N.A.
				[111]	TRY
Vicia narbonensis	Fabaceae	Fabales	C_3	[90,100]	N.A.
				This study	N.A.
Vicia peregrina	Fabaceae	Fabales	C_3	[105]	TRY
				[90]	N.A.
Vigna unguiculata	Fabaceae	Fabales	C_3	[90,92,136]	TRY
				[100]	N.A.
				[4]	BIEN
Viola arvensis	Violaceae	Malpighiales	C_3	[90]	N.A.
Vulpia bromoides	Poaceae	Poales	C_3	[93]	TRY
				[90]	N.A.
Vulpia ciliata	Poaceae	Poales	C_3	[1,93]	TRY
				[90]	N.A.
Vulpia microstachys	Poaceae	Poales	C_3	[7]	BIEN
Vulpia myuros	Poaceae	Poales	C_3	[106]	AusTraits
				[90,94]	N.A.
				[7]	BIEN
Waitzia acuminata	Asteraceae	Asterales	C_3	[106]	AusTraits
Whiteochloa multiciliata	Poaceae	Poales	C_4	[114,136]	TRY

Xanthisma gracile	Asteraceae	Asterales	C_3	101	TRY
				90	N.A.
Xanthium orientale	Asteraceae	Asterales	C_3	90	N.A.
				16	TRY
Xanthium strumarium	Asteraceae	Asterales	C_3	22,26,91,92,96	TRY
				4	BIEN
				90	N.A.
Zea mays	Poaceae	Poales	C_4	1,66,77,92,136	TRY
				4	BIEN
				90,94	N.A.
Zornia glochidiata	Fabaceae	Fabales	C_3	67	TRY
				90	N.A.

(d) Specific leaf area

Species	Family	Order	Type	Reference	Database
Abelmoschus esculentus	Malvaceae	Malvales	C_3	[142]	N.A.
				This study	N.A.
Abutilon theophrasti	Malvaceae	Malvales	C_3	[2]	TRY
Achyrachaena mollis	Asteraceae	Asterales	C_3	[143]	BIEN
Acmispon brachycarpus	Fabaceae	Fabales	C_3	[143,144]	BIEN
Aconitum gymnandrum	Ranunculaceae	Ranunculales	C_3	[5]	BIEN
				[145]	TRY
Actinobole uliginosum	Asteraceae	Asterales	C_3	[106,146,147]	AusTraits
				[145]	TRY
Aegilops geniculata	Poaceae	Poales	C_3	[148,149]	LEDA
				[2]	TRY
Aegilops neglecta	Poaceae	Poales	C_3	[1,145]	TRY
Aegilops speltoides	Poaceae	Poales	C_3	[150,151]	N.A.
Aegilops tauschii	Poaceae	Poales	C_3	[150]	N.A.
Aegilops triuncialis	Poaceae	Poales	C_3	[7]	BIEN
Agoseris heterophylla	Asteraceae	Asterales	C_3	[144]	BIEN
Agriophyllum squarrosum	Amaranthaceae	Caryophyllales	C_4	[96]	TRY
Agrostis muelleriana	Poaceae	Poales	C_3	[152]	AusTraits
Agrostis scabra	Poaceae	Poales	C_3	[2,153]	TRY
				[98]	BIEN
Aira caryophyllea	Poaceae	Poales	C_3	[7,98]	BIEN
Aira cupaniana	Poaceae	Poales	C_3	[146]	AusTraits
Aira elegantissima	Poaceae	Poales	C_3	[154]	AusTraits
Aira praecox	Poaceae	Poales	C_3	[98]	BIEN
Alloteropsis cimicina	Poaceae	Poales	C_4	[151]	N.A.
Alopecurus myosuroides	Poaceae	Poales	C_3	[155]	LEDA
Alopecurus utriculatus	Poaceae	Poales	C_3	[93]	TRY
Alyssum alyssoides	Brassicaceae	Brassicales	C_3	[156]	BIEN

Alyssum linifolium	Brassicaceae	Brassicales	C_3	[147]	AusTraits
				[145]	TRY
Amaranthus blitoides	Amaranthaceae	Caryophyllales	C_4	[157]	LEDA
				[2]	TRY
Amaranthus cruentus	Amaranthaceae	Caryophyllales	C_4	[142]	N.A.
				This study	N.A.
Amaranthus hybridus	Amaranthaceae	Caryophyllales	C_4	[142]	N.A.
Amaranthus retroflexus	Amaranthaceae	Caryophyllales	C_4	[157]	LEDA
				[1,2]	TRY
Amsinckia menziesii	Boraginaceae	Boraginales	C_3	[98,144]	BIEN
Anacyclus clavatus	Asteraceae	Asterales	C_3	[158]	BIEN
Androsace septentrionalis	Primulaceae	Ericales	C_3	[153]	TRY
Anthemis arvensis	Asteraceae	Asterales	C_3	[98,158]	BIEN
Anthriscus caucalis	Apiaceae	Apiales	C_3	[98]	BIEN
Anthyllis vulneraria	Fabaceae	Fabales	C_3	[102]	TRY
				[159]	BIEN
Arabidopsis thaliana	Brassicaceae	Brassicales	C_3	[98]	BIEN
				[18–21]	N.A.
Arachis hypogaea	Fabaceae	Fabales	C_3	[142]	N.A.
				This study	N.A.
Arachis monticola	Fabaceae	Fabales	C_3	[142]	N.A.
				This study	N.A.
Arctotheca calendula	Asteraceae	Asterales	C_3	[146,154]	AusTraits
Arenaria serpyllifolia	Caryophyllaceae	Caryophyllales	C_3	[98]	BIEN
				[107]	TRY
Aristida funiculata	Poaceae	Poales	C_4	[151]	N.A.
Artemisia scoparia	Asteraceae	Asterales	C_3	[108]	BIEN
				[96,145]	TRY
Aster subulatus	Asteraceae	Asterales	C_3	[160]	AusTraits
Astragalus gambelianus	Fabaceae	Fabales	C_3	[144]	BIEN
Astragalus pelecinus	Fabaceae	Fabales	C_3	[158]	BIEN

Athysanus pusillus	Brassicaceae	Brassicales	C_3	143	BIEN
Atriplex angulata	Amaranthaceae	Caryophyllales	C_4	147	AusTraits
				145	TRY
Avena barbata	Poaceae	Poales	C_3	7,158	BIEN
				106,146,154,161	AusTraits
				148,149,162	LEDA
				1,145	TRY
Avena fatua	Poaceae	Poales	C_3	160	AusTraits
				7,98	BIEN
				150,151	N.A.
				155	LEDA
Avena sativa	Poaceae	Poales	C_3	160	AusTraits
				142,150,151,163	N.A.
				157	LEDA
				This study	N.A.
				164	TRY
				7	BIEN
Avena sterilis	Poaceae	Poales	C_3	93	TRY
				142,150,163	N.A.
				This study	N.A.
Avena strigosa	Poaceae	Poales	C_3	164	TRY
Axyris amaranthoides	Amaranthaceae	Caryophyllales	C_4	23	TRY
Bellardia trixago	Orobanchaceae	Lamiales	C_3	158	BIEN
Bellida graminea	Asteraceae	Asterales	C_3	146	AusTraits
Beta vulgaris	Amaranthaceae	Caryophyllales	C_3	25,70,163	N.A.
				157	LEDA
				2,16	TRY
Blennospora drummondii	Asteraceae	Asterales	C_3	146	AusTraits
Borago officinalis	Boraginaceae	Boraginales	C_3	142	N.A.
				This study	N.A.
Bouteloua aristidoides	Poaceae	Poales	C_4	145	TRY

Brachiaria lata	Poaceae	Poales	C_4	151	N.A.
Brachypodium distachyon	Poaceae	Poales	C_3	1,2,93,145	TRY
Brachyscome curvicarpa	Asteraceae	Asterales	C_3	147	AusTraits
				145	TRY
Brachyscome iberidifolia	Asteraceae	Asterales	C_3	106,146	AusTraits
Brachyscome perpusilla	Asteraceae	Asterales	C_3	146	AusTraits
Brassica carinata	Brassicaceae	Brassicales	C_3	164	TRY
Brassica juncea	Brassicaceae	Brassicales	C_3	164	TRY
Brassica napus	Brassicaceae	Brassicales	C_3	155,157	LEDA
				28,29,31,36	N.A.
				145,164	TRY
Brassica oleracea	Brassicaceae	Brassicales	C_3	25,142,163	N.A.
				157,165	LEDA
				This study	N.A.
Brassica rapa	Brassicaceae	Brassicales	C_3	98	BIEN
				166	LEDA
				164	TRY
Brassica tournefortii	Brassicaceae	Brassicales	C_3	146,147	AusTraits
				145	TRY
Briza maxima	Poaceae	Poales	C_3	33,146,154	AusTraits
				151	N.A.
				7	BIEN
Briza minor	Poaceae	Poales	C_3	154	AusTraits
Bromus brachystachys	Poaceae	Poales	C_3	150	N.A.
Bromus carinatus	Poaceae	Poales	C_3	7,98,143	BIEN
Bromus commutatus	Poaceae	Poales	C_3	98	BIEN
Bromus diandrus	Poaceae	Poales	C_3	7,143,144	BIEN
Bromus hordeaceus	Poaceae	Poales	C_3	7,98,143,144,158	BIEN
				162,167	LEDA
				1,71,145	TRY
				154	AusTraits

Bromus lanceolatus	Poaceae	Poales	C_3	148,162	LEDA
				1,2,93,145	TRY
Bromus madritensis	Poaceae	Poales	C_3	162	LEDA
				1,107,145	TRY
				144	BIEN
Bromus pumilio	Poaceae	Poales	C_3	151	N.A.
Bromus rigidus	Poaceae	Poales	C_3	158	BIEN
Bromus rubens	Poaceae	Poales	C_3	158	BIEN
				106,146	AusTraits
Bromus sterilis	Poaceae	Poales	C_3	93	TRY
				98	BIEN
				155	LEDA
Bromus tectorum	Poaceae	Poales	C_3	98,158	BIEN
Buglossoides arvensis	Boraginaceae	Boraginales	C_3	98	BIEN
Bulbine semibarbata	Asphodelaceae	Asparagales	C_3	146,147	AusTraits
				145	TRY
Calotis hispidula	Asteraceae	Asterales	C_3	146,147	AusTraits
				145	TRY
Calotis inermis	Asteraceae	Asterales	C_3	147	AusTraits
				145	TRY
Calotis plumulifera	Asteraceae	Asterales	C_3	146	AusTraits
Calystegia sepium	Convolvulaceae	Solanales	C_3	168	LEDA
Camelina sativa	Brassicaceae	Brassicales	C_3	164	TRY
Capsicum annuum	Solanaceae	Solanales	C_3	157	LEDA
				35,117,163	N.A.
				16	TRY
Cardamine flexuosa	Brassicaceae	Brassicales	C_3	98	BIEN
Carduus pycnocephalus	Asteraceae	Asterales	C_3	144	BIEN
Carthamus glaucus	Asteraceae	Asterales	C_3	93	TRY
Catapodium rigidum	Poaceae	Poales	C_3	1,145	TRY
Cenchrus brownii	Poaceae	Poales	C_4	151	N.A.

Cenchrus echinatus	Poaceae	Poales	C_4	151	N.A.
Cenchrus pilosus	Poaceae	Poales	C_4	151	N.A.
Centaurea melitensis	Asteraceae	Asterales	C_3	144	BIEN
Centaurea solstitialis	Asteraceae	Asterales	C_3	156	BIEN
Centrolepis aristata	Restionaceae	Poales	C_3	146,169,170	AusTraits
Centrolepis strigosa	Restionaceae	Poales	C_3	169	AusTraits
Cephalipterum drummondii	Asteraceae	Asterales	C_3	146	AusTraits
Cerastium glomeratum	Caryophyllaceae	Caryophyllales	C_3	98	BIEN
Cerastium pumilum	Caryophyllaceae	Caryophyllales	C_3	98	BIEN
Cerastium semidecandrum	Caryophyllaceae	Caryophyllales	C_3	98	BIEN
Ceratogyne obionoides	Asteraceae	Asterales	C_3	146	AusTraits
Chenopodium acuminatum	Amaranthaceae	Caryophyllales	C_3	96,145	TRY
Chenopodium ficifolium	Amaranthaceae	Caryophyllales	C_3	159	BIEN
Chenopodium vulvaria	Amaranthaceae	Caryophyllales	C_3	156	BIEN
				96	TRY
Chloris pectinata	Poaceae	Poales	C_4	147	AusTraits
				145	TRY
Chloris virgata	Poaceae	Poales	C_4	147	AusTraits
				96,145	TRY
Chthonocephalus pseudevax	Asteraceae	Asterales	C_3	146	AusTraits
Chylismia brevipes	Onagraceae	Myrtales	C_3	2	TRY
Chylismia claviformis	Onagraceae	Myrtales	C_3	2	TRY
Cicer arietinum	Fabaceae	Fabales	C_3	150,163	N.A.
Cicer judaicum	Fabaceae	Fabales	C_3	150	N.A.
Cicer reticulatum	Fabaceae	Fabales	C_3	150,163	N.A.
Cladanthus mixtus	Asteraceae	Asterales	C_3	158	BIEN
Clarkia purpurea	Onagraceae	Myrtales	C_3	143,144	BIEN
Claytonia parviflora	Montiaceae	Caryophyllales	C_3	143	BIEN
Claytonia perfoliata	Montiaceae	Caryophyllales	C_3	98,143	BIEN
Coix lacryma-jobi	Poaceae	Poales	C_4	151	N.A.
Collomia heterophylla	Polemoniaceae	Ericales	C_3	143	BIEN

Conringia orientalis	Brassicaceae	Brassicales	C_3	98	BIEN
Conyza canadensis	Asteraceae	Asterales	C_3	171	LEDA
				159,172	BIEN
Cordylanthus tenuis	Orobanchaceae	Lamiales	C_3	143	BIEN
Craspedia variabilis	Asteraceae	Asterales	C_3	169,170	AusTraits
Crepis biennis	Asteraceae	Asterales	C_3	71	TRY
				173	BIEN
Crepis capillaris	Asteraceae	Asterales	C_3	98,158	BIEN
Crepis foetida	Asteraceae	Asterales	C_3	107	TRY
Crepis nicaeensis	Asteraceae	Asterales	C_3	96	TRY
Crepis occidentalis	Asteraceae	Asterales	C_3	174	BIEN
Crepis sancta	Asteraceae	Asterales	C_3	148	LEDA
Crepis vesicaria	Asteraceae	Asterales	C_3	158	BIEN
				148	LEDA
Cucumis sativus	Cucurbitaceae	Cucurbitales	C_3	36	N.A.
				16	TRY
Cymbonotus lawsonianus	Asteraceae	Asterales	C_3	154	AusTraits
Cynosurus echinatus	Poaceae	Poales	C_3	154	AusTraits
				7	BIEN
Cyperus flavidus	Cyperaceae	Poales	C_4	37	TRY
Dactyloctenium aegyptium	Poaceae	Poales	C_4	151	N.A.
Dactyloctenium giganteum	Poaceae	Poales	C_4	151	N.A.
Dactyloctenium radulans	Poaceae	Poales	C_4	175	AusTraits
				151	N.A.
Danthoniopsis dinteri	Poaceae	Poales	C_4	151	N.A.
Dasypyrum villosum	Poaceae	Poales	C_3	151	N.A.
Daucus glochidiatus	Apiaceae	Apiales	C_3	146,147,154,169,170	AusTraits
				145	TRY
Digitaria ciliaris	Poaceae	Poales	C_4	151	N.A.
Digitaria sanguinalis	Poaceae	Poales	C_4	160	AusTraits
				145	TRY

Digitaria setigera	Poaceae	Poales	C_4	[151]	N.A.
Diheteropogon hagerupii	Poaceae	Poales	C_4	[151]	N.A.
Diplotaxis erucoides	Brassicaceae	Brassicales	C_3	[151]	N.A.
Diplotaxis ibicensis	Brassicaceae	Brassicales	C_3	[176]	LEDA
				[70]	N.A.
				[16]	TRY
Dontostemon micranthus	Brassicaceae	Brassicales	C_3	[108]	BIEN
Draba verna	Brassicaceae	Brassicales	C_3	[98]	BIEN
Dysphania aristata	Amaranthaceae	Caryophyllales	C_3	[96]	TRY
Dysphania melanocarpa	Amaranthaceae	Caryophyllales	C_3	[175]	AusTraits
Echinochloa cruspavonis	Poaceae	Poales	C_4	[151]	N.A.
Echinochloa frumentacea	Poaceae	Poales	C_4	[151]	N.A.
Echinochloa muricata	Poaceae	Poales	C_4	[151]	N.A.
Echinochloa oryzoides	Poaceae	Poales	C_4	[151]	N.A.
Echinochloa stagnina	Poaceae	Poales	C_4	[151]	N.A.
Echium plantagineum	Boraginaceae	Boraginales	C_3	[158]	BIEN
				[146,160]	AusTraits
				[16]	TRY
				[177]	LEDA
Ehrharta longiflora	Poaceae	Poales	C_3	[146]	AusTraits
Eleusine coracana	Poaceae	Poales	C_4	[151]	N.A.
Eleusine indica	Poaceae	Poales	C_4	[145]	TRY
				[151]	N.A.
Enneapogon avenaceus	Poaceae	Poales	C_4	[178]	AusTraits
Enneapogon polyphyllus	Poaceae	Poales	C_4	[147]	AusTraits
				[145]	TRY
Enteropogon prieurii	Poaceae	Poales	C_4	[151]	N.A.
Epaltes australis	Asteraceae	Asterales	C_3	[106]	AusTraits
Epilobium minutum	Onagraceae	Myrtales	C_3	[143]	BIEN
Eragrostis cilianensis	Poaceae	Poales	C_4	[96]	TRY
				[151]	N.A.

				[178]	AusTraits
Eragrostis mexicana	Poaceae	Poales	C_4	[151]	N.A.
Eragrostis minor	Poaceae	Poales	C_4	[96]	TRY
Eragrostis pectinacea	Poaceae	Poales	C_4	[151]	N.A.
Eragrostis pilosa	Poaceae	Poales	C_4	[151]	N.A.
Eragrostis unioloides	Poaceae	Poales	C_4	[151]	N.A.
Eremopyrum bonaepartis	Poaceae	Poales	C_3	[150]	N.A.
Eremopyrum orientale	Poaceae	Poales	C_3	[150]	N.A.
Eremopyrum triticeum	Poaceae	Poales	C_3	[151]	N.A.
Eriachne aristidea	Poaceae	Poales	C_4	[151]	N.A.
Erigeron annuus	Asteraceae	Asterales	C_3	[165]	LEDA
Erodium aureum	Geraniaceae	Geraniales	C_3	[146]	AusTraits
Erodium botrys	Geraniaceae	Geraniales	C_3	[106]	AusTraits
Erodium ciconium	Geraniaceae	Geraniales	C_3	[93]	TRY
Erodium crinitum	Geraniaceae	Geraniales	C_3	[175]	AusTraits
Erodium cygnorum	Geraniaceae	Geraniales	C_3	[146,178]	AusTraits
Erodium moschatum	Geraniaceae	Geraniales	C_3	[144]	BIEN
Erodium stephanianum	Geraniaceae	Geraniales	C_3	[96,145]	TRY
Eruca vesicaria	Brassicaceae	Brassicales	C_3	[163]	N.A.
				[164]	TRY
Erymophyllum ramosum	Asteraceae	Asterales	C_3	[146]	AusTraits
Erymophyllum tenellum	Asteraceae	Asterales	C_3	[106]	AusTraits
Euchiton sphaericus	Asteraceae	Asterales	C_3	[160]	AusTraits
Euphorbia drummondii	Euphorbiaceae	Malpighiales	C_4	[147,175]	AusTraits
				[145]	TRY
Euphorbia humifusa	Euphorbiaceae	Malpighiales	C_4	[2,96,145]	TRY
Euphorbia maculata	Euphorbiaceae	Malpighiales	C_4	[179]	TRY
Fagopyrum esculentum	Polygonaceae	Caryophyllales	C_3	[164]	TRY
Festuca incurva	Poaceae	Poales	C_3	[158]	BIEN
Filago gallica	Asteraceae	Asterales	C_3	[144]	BIEN
Filago pyramidata	Asteraceae	Asterales	C_3	[158]	BIEN

Galium divaricatum	Rubiaceae	Gentianales	C_3	154	AusTraits
Galium parisiense	Rubiaceae	Gentianales	C_3	143	BIEN
Gentiana parvula	Gentianaceae	Gentianales	C_3	123	BIEN
Gentianella amarella	Gentianaceae	Gentianales	C_3	75	TRY
Gentianopsis paludosa	Gentianaceae	Gentianales	C_3	123	BIEN
Gilberta tenuifolia	Asteraceae	Asterales	C_3	146	AusTraits
Gilia capitata	Polemoniaceae	Ericales	C_3	143	BIEN
Gilia clivorum	Polemoniaceae	Ericales	C_3	144	BIEN
Glycine max	Fabaceae	Fabales	C_3	1	TRY
				20,163	N.A.
Gnaphalium affine	Asteraceae	Asterales	C_3	2,145	TRY
Gnaphalium luteoalbum	Asteraceae	Asterales	C_3	160,170	AusTraits
				5	BIEN
Gnephosis tenuissima	Asteraceae	Asterales	C_3	146	AusTraits
Gonocarpus nodulosus	Haloragaceae	Saxifragales	C_3	146	AusTraits
Goodenia berardiana	Goodeniaceae	Asterales	C_3	146	AusTraits
Goodenia cycloptera	Goodeniaceae	Asterales	C_3	147	AusTraits
				145	TRY
Goodenia havilandi	Goodeniaceae	Asterales	C_3	175	AusTraits
Grubovia dasyphylla	Amaranthaceae	Caryophyllales	C_4	96	TRY
Guizotia abyssinica	Asteraceae	Asterales	C_3	164	TRY
Halenia elliptica	Gentianaceae	Gentianales	C_3	123	BIEN
Harmsiodoxa blennodioides	Brassicaceae	Brassicales	C_3	147	AusTraits
				145	TRY
Harmsiodoxa brevipes	Brassicaceae	Brassicales	C_3	175	AusTraits
Harmsiodoxa puberula	Brassicaceae	Brassicales	C_3	147	AusTraits
				145	TRY
Helianthus agrestis	Asteraceae	Asterales	C_3	39	BIEN
Helianthus annuus	Asteraceae	Asterales	C_3	157	LEDA
				1,16,145,164	TRY
				39	BIEN

				25,35,40,163	N.A.
Helianthus argophyllus	Asteraceae	Asterales	C_3	39	BIEN
Helianthus debilis	Asteraceae	Asterales	C_3	39	BIEN
Helianthus neglectus	Asteraceae	Asterales	C_3	39	BIEN
Helianthus praecox	Asteraceae	Asterales	C_3	39	BIEN
Heliotropium europaeum	Boraginaceae	Boraginales	C_3	175	AusTraits
Hesperolinon micranthum	Linaceae	Malpighiales	C_3	143	BIEN
Hordeum marinum	Poaceae	Poales	C_3	150	N.A.
Hordeum murinum	Poaceae	Poales	C_3	98,144,158	BIEN
				106,146,147,178	AusTraits
				162	LEDA
				1,145	TRY
Hordeum spontaneum	Poaceae	Poales	C_3	93	TRY
				142,150,151,163	N.A.
Hordeum vulgare	Poaceae	Poales	C_3	142,150,151,163	N.A.
				180	LEDA
Hyalosperma demissum	Asteraceae	Asterales	C_3	146	AusTraits
Hyalosperma glutinosum	Asteraceae	Asterales	C_3	146	AusTraits
Hyalosperma semisterile	Asteraceae	Asterales	C_3	147	AusTraits
				145	TRY
Hydrocotyle callicarpa	Araliaceae	Apiales	C_3	170	AusTraits
Hydrocotyle foveolata	Araliaceae	Apiales	C_3	169,170	AusTraits
Hydrocotyle pilifera	Araliaceae	Apiales	C_3	146	AusTraits
Hypecoum leptocarpum	Papaveraceae	Ranunculales	C_3	123	BIEN
Hypericum gramineum	Hypericaceae	Malpighiales	C_3	124,154,170,181	AusTraits
Hypochaeris glabra	Asteraceae	Asterales	C_3	146,154,160	AusTraits
				98,144	BIEN
Impatiens capensis	Balsaminaceae	Ericales	C_3	37,179	TRY
				165	LEDA
Impatiens furcillata	Balsaminaceae	Ericales	C_3	96	TRY
Ipomoea purpurea	Convolvulaceae	Solanales	C_3	145	TRY

Isatis lusitanica	Brassicaceae	Brassicales	C_3	93	TRY
Ischaemum rugosum	Poaceae	Poales	C_4	151	N.A.
Isoetopsis graminifolia	Asteraceae	Asterales	C_3	146,147	AusTraits
				145	TRY
Ixeris chinensis	Asteraceae	Asterales	C_3	96	TRY
Jacobaea vulgaris	Asteraceae	Asterales	C_3	98	BIEN
				145	TRY
Kali collinum	Amaranthaceae	Caryophyllales	C_4	23,96,145	TRY
				108	BIEN
Kalimeris altaica	Asteraceae	Asterales	C_3	96,145	TRY
Kickxia spuria	Plantaginaceae	Lamiales	C_3	148	LEDA
Kummerowia striata	Fabaceae	Fabales	C_3	96	TRY
Lachnagrostis filiformis	Poaceae	Poales	C_3	160,170,181	AusTraits
Lachnagrostis meionectes	Poaceae	Poales	C_3	152	AusTraits
Lactuca indica	Asteraceae	Asterales	C_3	145	TRY
Lactuca ludoviciana	Asteraceae	Asterales	C_3	2,145	TRY
Lactuca saligna	Asteraceae	Asterales	C_3	160	AusTraits
Lactuca sativa	Asteraceae	Asterales	C_3	142	N.A.
				157	LEDA
				This study	N.A.
Lactuca serriola	Asteraceae	Asterales	C_3	160	AusTraits
				98,143,144,156,159	BIEN
				142	N.A.
				This study	N.A.
Lamarckia aurea	Poaceae	Poales	C_3	158	BIEN
Lamium purpureum	Lamiaceae	Lamiales	C_3	98	BIEN
Lapsana communis	Asteraceae	Asterales	C_3	98,159	BIEN
Lapsanastrum humile	Asteraceae	Asterales	C_3	127	TRY
Lasthenia californica	Asteraceae	Asterales	C_3	144	BIEN
Lathyrus aphaca	Fabaceae	Fabales	C_3	93	TRY
Lathyrus cicera	Fabaceae	Fabales	C_3	142,163	N.A.

Lathyrus sativus	Fabaceae	Fabales	C_3	142,163	N.A.
				164	TRY
Lawrencella rosea	Asteraceae	Asterales	C_3	146	AusTraits
Lens culinaris	Fabaceae	Fabales	C_3	142,150	N.A.
Lepidium nitidum	Brassicaceae	Brassicales	C_3	144	BIEN
Leptochloa fusca	Poaceae	Poales	C_4	160	AusTraits
Leptochloa panicoides	Poaceae	Poales	C_4	151	N.A.
Leptochloa virgata	Poaceae	Poales	C_4	151	N.A.
Leptosiphon ciliatus	Polemoniaceae	Ericales	C_3	143	BIEN
Levenhookia dubia	Stylidiaceae	Asterales	C_3	146	AusTraits
Linaria pelisseriana	Plantaginaceae	Lamiales	C_3	154	AusTraits
Linum stelleroides	Linaceae	Malpighiales	C_3	96,145	TRY
Linum usitatissimum	Linaceae	Malpighiales	C_3	142	N.A.
Lipandra polysperma	Amaranthaceae	Caryophyllales	C_3	156	BIEN
Lobelia gibbosa	Campanulaceae	Asterales	C_3	146	AusTraits
Lolium rigidum	Poaceae	Poales	C_3	158	BIEN
				162	LEDA
				1,93,145	TRY
				154	AusTraits
Lolium X	Poaceae	Poales	C_3	164	TRY
Lotus angustissimus	Fabaceae	Fabales	C_3	160	AusTraits
Lotus corniculatus	Fabaceae	Fabales	C_3	98,159,182	BIEN
				148,149	LEDA
				71	TRY
Loudetiopsis kerstingii	Poaceae	Poales	C_4	151	N.A.
Lupinus bicolor	Fabaceae	Fabales	C_3	144	BIEN
Lupinus nanus	Fabaceae	Fabales	C_3	144	BIEN
Lythrum hyssopifolia	Lythraceae	Myrtales	C_3	160,181	AusTraits
Madia elegans	Asteraceae	Asterales	C_3	143	BIEN
Malva pusilla	Malvaceae	Malvales	C_3	183	LEDA
Medicago polymorpha	Fabaceae	Fabales	C_3	146	AusTraits

Melinis repens	Poaceae	Poales	C_4	[93]	TRY
				[144]	BIEN
				[147]	AusTraits
				[2,145]	TRY
				[151]	N.A.
Mentzelia dispersa	Loasaceae	Cornales	C_3	[143]	BIEN
Micropus californicus	Asteraceae	Asterales	C_3	[144]	BIEN
Microstegium vimineum	Poaceae	Poales	C_4	[37]	TRY
Millotia myosotidifolia	Asteraceae	Asterales	C_3	[146]	AusTraits
Moenchia erecta	Caryophyllaceae	Caryophyllales	C_3	[154]	AusTraits
Mollugo verticillata	Molluginaceae	Caryophyllales	C_4	[160]	AusTraits
Montia fontana	Montiaceae	Caryophyllales	C_3	[98]	BIEN
Muhlenbergia peruviana	Poaceae	Poales	C_4	[145]	TRY
Myosotis discolor	Boraginaceae	Boraginales	C_3	[98]	BIEN
				[154]	AusTraits
Myosurus minimus	Ranunculaceae	Ranunculales	C_3	[98]	BIEN
Myriocephalus rhizocephalus	Asteraceae	Asterales	C_3	[147]	AusTraits
				[145]	TRY
Navarretia jaredii	Polemoniaceae	Ericales	C_3	[144]	BIEN
Neatostema apulum	Boraginaceae	Boraginales	C_3	[158]	BIEN
Nemophila heterophylla	Boraginaceae	Boraginales	C_3	[143]	BIEN
Nicotiana rotundifolia	Solanaceae	Solanales	C_3	[146]	AusTraits
Ochthodium aegyptiacum	Brassicaceae	Brassicales	C_3	[93]	TRY
Ocimum basilicum	Lamiaceae	Lamiales	C_3	[16]	TRY
				[35]	N.A.
Omphalolappula concava	Boraginaceae	Boraginales	C_3	[146,147]	AusTraits
				[145]	TRY
Ornithopus compressus	Fabaceae	Fabales	C_3	[158]	BIEN
Oryza barthii	Poaceae	Poales	C_3	[151]	N.A.
Oryza eichingeri	Poaceae	Poales	C_3	[151]	N.A.
Oryza glaberrima	Poaceae	Poales	C_3	[151]	N.A.

Oryza grandiglumis	Poaceae	Poales	C_3	[151]	N.A.
Oryza latifolia	Poaceae	Poales	C_3	[41]	N.A.
Oryza punctata	Poaceae	Poales	C_3	[41]	N.A.
Oryza rufipogon	Poaceae	Poales	C_3	[41,163]	N.A.
Oryza sativa	Poaceae	Poales	C_3	[20,36,40,41,43,44,46,49–51,53,163]	N.A.
				[1]	TRY
Osteospermum monstrosum	Asteraceae	Asterales	C_3	[146]	AusTraits
Oxybasis glauca	Amaranthaceae	Caryophyllales	C_4	[23,96]	TRY
Oxychloris scariosa	Poaceae	Poales	C_4	[151]	N.A.
Panicum bisulcatum	Poaceae	Poales	C_3	[151]	N.A.
Panicum capillare	Poaceae	Poales	C_4	[171,184]	LEDA
				[2]	TRY
Panicum dichotomiflorum	Poaceae	Poales	C_4	[151]	N.A.
Panicum flexuosum	Poaceae	Poales	C_4	[151]	N.A.
Panicum hirticaule	Poaceae	Poales	C_4	[151]	N.A.
Panicum laetum	Poaceae	Poales	C_4	[151]	N.A.
Panicum miliaceum	Poaceae	Poales	C_4	[151]	N.A.
Papaver rhoeas	Papaveraceae	Ranunculales	C_3	[155]	LEDA
Parahyparrhenia annua	Poaceae	Poales	C_4	[164]	TRY
Parakeelya corrigioloides	Montiaceae	Caryophyllales	C_3	[146]	AusTraits
Parakeelya eremaea	Montiaceae	Caryophyllales	C_3	[146,147]	AusTraits
				[145]	TRY
Parakeelya nana	Montiaceae	Caryophyllales	C_3	[146]	AusTraits
Parakeelya ptychosperma	Montiaceae	Caryophyllales	C_3	[175]	AusTraits
Parentucellia latifolia	Orobanchaceae	Lamiales	C_3	[146,154]	AusTraits
Pennisetum glaucum	Poaceae	Poales	C_4	[142,163]	N.A.
				[145]	TRY
				This study	N.A.
Pennisetum sieberianum	Poaceae	Poales	C_4	[151]	N.A.
Pennisetum violaceum	Poaceae	Poales	C_4	[151]	N.A.
Pentameris airoides	Poaceae	Poales	C_3	[106,146]	AusTraits

Persicaria bungeana	Polygonaceae	Caryophyllales	C_3	[2]	TRY
Persicaria lapathifolia	Polygonaceae	Caryophyllales	C_3	[160]	AusTraits
				[184,185]	LEDA
Persicaria maculosa	Polygonaceae	Caryophyllales	C_3	[156]	BIEN
				[165,167]	LEDA
				[145]	TRY
Persicaria posumbu	Polygonaceae	Caryophyllales	C_3	[179]	TRY
Petrorhagia dubia	Caryophyllaceae	Caryophyllales	C_3	[146]	AusTraits
Petrorhagia nanteuilii	Caryophyllaceae	Caryophyllales	C_3	[158]	BIEN
				[154]	AusTraits
Phalaris minor	Poaceae	Poales	C_3	[160]	AusTraits
Phalaris paradoxa	Poaceae	Poales	C_3	[93]	TRY
				[150]	N.A.
Phaseolus vulgaris	Fabaceae	Fabales	C_3	[35,55,56]	N.A.
				[1,16,133]	TRY
Phlegmatospermum cochlearinum	Brassicaceae	Brassicales	C_3	[147]	AusTraits
				[145]	TRY
Phlox gracilis	Polemoniaceae	Ericales	C_3	[143]	BIEN
Phoebanthus tenuifolius	Asteraceae	Asterales	C_3	[39]	BIEN
Phyllangium sulcatum	Loganiaceae	Gentianales	C_3	[146]	AusTraits
Pimelea simplex	Thymelaeaceae	Malvales	C_3	[175]	AusTraits
Pimpinella cretica	Apiaceae	Apiales	C_3	[93]	TRY
Pisum fulvum	Fabaceae	Fabales	C_3	[150]	N.A.
Pisum sativum	Fabaceae	Fabales	C_3	[157]	LEDA
				[25,150,163]	N.A.
				[164]	TRY
Plagiobothrys nothofulvus	Boraginaceae	Boraginales	C_3	[144]	BIEN
Plantago debilis	Plantaginaceae	Lamiales	C_3	[146,170,175]	AusTraits
Plantago erecta	Plantaginaceae	Lamiales	C_3	[144]	BIEN
Plantago lagopus	Plantaginaceae	Lamiales	C_3	[158]	BIEN
Plantago major	Plantaginaceae	Lamiales	C_3	[98,159]	BIEN

Poa annua	Poaceae	Poales	C_3	165,167,177,184–186	LEDA
				16,145	TRY
				98,159	BIEN
				1,145	TRY
				155	LEDA
Podolepis canescens	Asteraceae	Asterales	C_3	146	AusTraits
Podolepis lessonii	Asteraceae	Asterales	C_3	106,146	AusTraits
Podotheca angustifolia	Asteraceae	Asterales	C_3	146	AusTraits
Podotheca gnaphalioides	Asteraceae	Asterales	C_3	146	AusTraits
Pogonolepis muelleriana	Asteraceae	Asterales	C_3	146	AusTraits
Polycnemum arvense	Amaranthaceae	Caryophyllales	C_3	96	TRY
Polygonum aviculare	Polygonaceae	Caryophyllales	C_4	160	AusTraits
				98	BIEN
				96	TRY
				155	LEDA
Poranthera microphylla	Phyllanthaceae	Malpighiales	C_3	146,169,170,187	AusTraits
Ptilotus gaudichaudii	Amaranthaceae	Caryophyllales	C_3	146,147,175	AusTraits
				145	TRY
Ranunculus sceleratus	Ranunculaceae	Ranunculales	C_3	160	AusTraits
				145	TRY
Raphanus raphanistrum	Brassicaceae	Brassicales	C_3	16,93,164	TRY
Raphanus sativus	Brassicaceae	Brassicales	C_3	177	LEDA
Rapistrum rugosum	Brassicaceae	Brassicales	C_3	93	TRY
Reseda phyteuma	Resedaceae	Brassicales	C_3	149	LEDA
Rhodanthe chlorocephala	Asteraceae	Asterales	C_3	146	AusTraits
Rhodanthe citrina	Asteraceae	Asterales	C_3	146	AusTraits
Rhodanthe laevis	Asteraceae	Asterales	C_3	146	AusTraits
Rhodanthe manglesii	Asteraceae	Asterales	C_3	146	AusTraits
Rhodanthe microglossa	Asteraceae	Asterales	C_3	147	AusTraits
				145	TRY
Rhodanthe polycephala	Asteraceae	Asterales	C_3	146	AusTraits

Rhodanthe polygalifolia	Asteraceae	Asterales	C_3	147	AusTraits
				145	TRY
Rhodanthe pygmaea	Asteraceae	Asterales	C_3	146	AusTraits
Rhodanthe spicata	Asteraceae	Asterales	C_3	146	AusTraits
Rhodanthe stricta	Asteraceae	Asterales	C_3	147	AusTraits
				145	TRY
Roepera iodocarpa	Zygophyllaceae	Zygophyllales	C_3	146,147,175	AusTraits
				145	TRY
Rorippa palustris	Brassicaceae	Brassicales	C_3	160	AusTraits
Rostraria cristata	Poaceae	Poales	C_3	2,23,145	TRY
				5,123	BIEN
				151	N.A.
Rostraria pumila	Poaceae	Poales	C_3	146	AusTraits
Rudbeckia hirta	Asteraceae	Asterales	C_3	172	BIEN
				165,186	LEDA
Sabulina douglasii	Caryophyllaceae	Caryophyllales	C_3	143	BIEN
Salicornia europaea	Amaranthaceae	Caryophyllales	C_3	96	TRY
Scandix iberica	Apiaceae	Apiales	C_3	93	TRY
Schoenia cassiniana	Asteraceae	Asterales	C_3	146	AusTraits
Schoenus apogon	Cyperaceae	Poales	C_3	169,181	AusTraits
Scolymus maculatus	Asteraceae	Asterales	C_3	93	TRY
Secale cereale	Poaceae	Poales	C_3	150,151,163	N.A.
				164	TRY
Secale vavilovii	Poaceae	Poales	C_3	150	N.A.
Senecio biserratus	Asteraceae	Asterales	C_3	169	AusTraits
Senecio glomeratus	Asteraceae	Asterales	C_3	169	AusTraits
Senecio glossanthus	Asteraceae	Asterales	C_3	147	AusTraits
				145	TRY
Senecio sylvaticus	Asteraceae	Asterales	C_3	98,156	BIEN
Sesamum indicum	Pedaliaceae	Lamiales	C_3	142,163	N.A.
				This study	N.A.

Setaria faberi	Poaceae	Poales	C_4	151	N.A.
Setaria helvola	Poaceae	Poales	C_4	171	LEDA
Setaria italica	Poaceae	Poales	C_4	151	N.A.
				164	TRY
Setaria verticillata	Poaceae	Poales	C_4	151	N.A.
Setaria viridis	Poaceae	Poales	C_4	96,145	TRY
				151	N.A.
Sigesbeckia orientalis	Asteraceae	Asterales	C_3	58,187	AusTraits
Silene nocturna	Caryophyllaceae	Caryophyllales	C_3	146	AusTraits
Sinapis alba	Brassicaceae	Brassicales	C_3	164	TRY
Sinapis arvensis	Brassicaceae	Brassicales	C_3	98	BIEN
				155,188	LEDA
Siphonostegia chinensis	Orobanchaceae	Lamiales	C_3	96	TRY
Sisymbrium cavanillesianum	Brassicaceae	Brassicales	C_3	158	BIEN
Solanum lycopersicum	Solanaceae	Solanales	C_3	25,59,142,163	N.A.
				60	BIEN
				This study	N.A.
Solanum physalifolium	Solanaceae	Solanales	C_3	160	AusTraits
Solanum pimpinellifolium	Solanaceae	Solanales	C_3	25,142,163	N.A.
				60	BIEN
				This study	N.A.
Sonchus asper	Asteraceae	Asterales	C_3	98,159	BIEN
Sonchus oleraceus	Asteraceae	Asterales	C_3	106,146,160	AusTraits
				98	BIEN
				96,145	TRY
Sorghum amplum	Poaceae	Poales	C_4	151	N.A.
Sorghum angustum	Poaceae	Poales	C_4	151	N.A.
Sorghum arundinaceum	Poaceae	Poales	C_4	142,151	N.A.
Sorghum bicolor	Poaceae	Poales	C_4	142,151,163	N.A.
				157	LEDA
Sorghum ecarinatum	Poaceae	Poales	C_4	151	N.A.

Sorghum timorense	Poaceae	Poales	C_4	[151]	N.A.
Spergularia purpurea	Caryophyllaceae	Caryophyllales	C_3	[158]	BIEN
Spergularia rubra	Caryophyllaceae	Caryophyllales	C_3	[98]	BIEN
Spinacia oleracea	Amaranthaceae	Caryophyllales	C_3	[35]	N.A.
Stephanomeria virgata	Asteraceae	Asterales	C_3	[143]	BIEN
Stipa capensis	Poaceae	Poales	C_3	[151]	N.A.
				[107]	TRY
Streptoglossa cylindriceps	Asteraceae	Asterales	C_3	[124]	AusTraits
Stuartina muelleri	Asteraceae	Asterales	C_3	[170]	AusTraits
Suaeda glauca	Amaranthaceae	Caryophyllales	C_4	[96]	TRY
Suaeda heterophylla	Amaranthaceae	Caryophyllales	C_4	[96]	TRY
Taeniatherum caputmedusae	Poaceae	Poales	C_3	[150]	N.A.
				[7]	BIEN
Teesdalia nudicaulis	Brassicaceae	Brassicales	C_3	[98]	BIEN
Thysanocarpus curvipes	Brassicaceae	Brassicales	C_3	[143]	BIEN
Tolpis barbata	Asteraceae	Asterales	C_3	[158]	BIEN
				[154]	AusTraits
Trachymene cyanopetala	Araliaceae	Apiales	C_3	[146]	AusTraits
Trachymene ornata	Araliaceae	Apiales	C_3	[146]	AusTraits
Trachymene pilosa	Araliaceae	Apiales	C_3	[146]	AusTraits
Tragus racemosus	Poaceae	Poales	C_4	[96]	TRY
				[151]	N.A.
Tribolium echinatum	Poaceae	Poales	C_3	[151]	N.A.
Tribulus terrestris	Zygophyllaceae	Zygophyllales	C_4	[96]	TRY
Trichostema lanceolatum	Lamiaceae	Lamiales	C_3	[144]	BIEN
Trifolium albopurpureum	Fabaceae	Fabales	C_3	[144]	BIEN
Trifolium angustifolium	Fabaceae	Fabales	C_3	[160]	AusTraits
				[148,149]	LEDA
				[107]	TRY
Trifolium arvense	Fabaceae	Fabales	C_3	[106,154,160]	AusTraits
Trifolium campestre	Fabaceae	Fabales	C_3	[160]	AusTraits

				[71]	TRY
Trifolium cherleri	Fabaceae	Fabales	C_3	[158]	BIEN
Trifolium ciliolatum	Fabaceae	Fabales	C_3	[144]	BIEN
Trifolium glomeratum	Fabaceae	Fabales	C_3	[158]	BIEN
				[146,154,160]	AusTraits
Trifolium gracilentum	Fabaceae	Fabales	C_3	[144]	BIEN
Trifolium microcephalum	Fabaceae	Fabales	C_3	[144]	BIEN
Trifolium pilulare	Fabaceae	Fabales	C_3	[93]	TRY
Trifolium purpureum	Fabaceae	Fabales	C_3	[93]	TRY
Trifolium repens	Fabaceae	Fabales	C_3	[98,159,173,174,182]	BIEN
				[160]	AusTraits
				[142,163]	N.A.
				[1,2,71,127,145,179]	TRY
				[167]	LEDA
Trifolium striatum	Fabaceae	Fabales	C_3	[158]	BIEN
				[154,160]	AusTraits
Trigonella alba	Fabaceae	Fabales	C_3	[2,145]	TRY
Trigonella foenum-graecum	Fabaceae	Fabales	C_3	[164]	TRY
Trigonella officinalis	Fabaceae	Fabales	C_3	[165,168,186]	LEDA
				[164]	TRY
Tripleurospermum inodorum	Asteraceae	Asterales	C_4	[155]	LEDA
Triptilodiscus pygmaeus	Asteraceae	Asterales	C_3	[154,169]	AusTraits
Trisetaria panicea	Poaceae	Poales	C_3	[158]	BIEN
Triticum aestivum	Poaceae	Poales	C_3	[20,36,61,64,65,151]	N.A.
				[160]	AusTraits
				[189]	TRY
				[155]	LEDA
Triticum dicoccoides	Poaceae	Poales	C_3	[93]	TRY
				[25,142,163]	N.A.
Triticum monococcum	Poaceae	Poales	C_3	[150,151]	N.A.
Triticum timopheevii	Poaceae	Poales	C_3	[151]	N.A.

Triticum turgidum	Poaceae	Poales	C_3	25,142,150,163	N.A.
				189	TRY
Urospermum picroides	Asteraceae	Asterales	C_3	146	AusTraits
Ursinia anthemoides	Asteraceae	Asterales	C_3	146	AusTraits
Valerianella locusta	Caprifoliaceae	Dipsacales	C_3	98	BIEN
Velleia cycnopotamica	Goodeniaceae	Asterales	C_3	146	AusTraits
Velleia rosea	Goodeniaceae	Asterales	C_3	146	AusTraits
Veronica arvensis	Plantaginaceae	Lamiales	C_3	98	BIEN
Veronica hederifolia	Plantaginaceae	Lamiales	C_3	145	TRY
Veronica persica	Plantaginaceae	Lamiales	C_3	156,159	BIEN
				155	LEDA
				107	TRY
Vicia ervilia	Fabaceae	Fabales	C_3	150	N.A.
Vicia faba	Fabaceae	Fabales	C_3	142,150	N.A.
				157	LEDA
				This study	N.A.
				164	TRY
Vicia narbonensis	Fabaceae	Fabales	C_3	142,150	N.A.
				This study	N.A.
Vigna unguiculata	Fabaceae	Fabales	C_3	163	N.A.
Vulpia bromoides	Poaceae	Poales	C_3	146,154,178	AusTraits
				98	BIEN
Vulpia ciliata	Poaceae	Poales	C_3	158	BIEN
				162	LEDA
				1,145	TRY
Vulpia microstachys	Poaceae	Poales	C_3	7,143	BIEN
Vulpia myuros	Poaceae	Poales	C_3	106,146	AusTraits
				7,98,143,144	BIEN
				151	N.A.
Vulpia octoflora	Poaceae	Poales	C_3	143	BIEN
Wahlenbergia gracilenta	Campanulaceae	Asterales	C_3	146,170	AusTraits

Waitzia acuminata	Asteraceae	Asterales	C_3	106,146	AusTraits
Waitzia nitida	Asteraceae	Asterales	C_3	146	AusTraits
Xanthium strumarium	Asteraceae	Asterales	C_3	96,179	TRY
Yabea microcarpa	Apiaceae	Apiales	C_3	144	BIEN
Zaluzianskya divaricata	Scrophulariaceae	Lamiales	C_3	146	AusTraits
Zea mays	Poaceae	Poales	C_4	157	LEDA
				189	TRY
				151,163	N.A.
Zornia glochidiata	Fabaceae	Fabales	C_3	67	TRY
Zygophyllum sonderi	Zygophyllaceae	Zygophyllales	C_3	145	TRY

(e) ^{13}C isotopic composition

Species	Family	Order	Type	Reference	Database
Abelmoschus esculentus	Malvaceae	Malvales	C_3	This study	N.A.
Abutilon theophrasti	Malvaceae	Malvales	C_3	[91]	TRY
Acalypha virginica	Euphorbiaceae	Malpighiales	C_3	[91]	TRY
Adenosma glutinosa	Plantaginaceae	Lamiales	C_3	[190]	TRY
Aegilops cylindrica	Poaceae	Poales	C_3	[91]	TRY
				[191]	N.A.
Aeluropus littoralis	Poaceae	Poales	C_4	[191]	N.A.
Agrostis clavata	Poaceae	Poales	C_3	[190]	TRY
				[191]	N.A.
Agrostis scabra	Poaceae	Poales	C_3	[191]	N.A.
Aira caryophyllea	Poaceae	Poales	C_3	[191]	N.A.
Aira elegantissima	Poaceae	Poales	C_3	[191]	N.A.
Alopecurus aequalis	Poaceae	Poales	C_3	[190]	TRY
				[191]	N.A.
Alopecurus carolinianus	Poaceae	Poales	C_3	[91]	TRY
Alopecurus geniculatus	Poaceae	Poales	C_3	[190]	TRY
Alopecurus japonicus	Poaceae	Poales	C_3	[191]	N.A.
Alysicarpus heterophyllus	Fabaceae	Fabales	C_3	[190]	TRY
Alysicarpus schomburgkii	Fabaceae	Fabales	C_3	[190]	TRY
Amaranthus cruentus	Amaranthaceae	Caryophyllales	C_3	This study	N.A.
Amaranthus retroflexus	Amaranthaceae	Caryophyllales	C_4	[190]	TRY
Amaranthus tuberculatus	Amaranthaceae	Caryophyllales	C_4	[91]	TRY
Androsace septentrionalis	Primulaceae	Ericales	C_3	[101]	TRY
Anthoxanthum aristatum	Poaceae	Poales	C_3	[191]	N.A.
Antinoria agrostidea	Poaceae	Poales	C_3	[191]	N.A.
Apera interrupta	Poaceae	Poales	C_3	[191]	N.A.

Apera spica-venti	Poaceae	Poales	C_3	[191]	N.A.
Arachis hypogaea	Fabaceae	Fabales	C_3	This study	N.A.
Arachis monticola	Fabaceae	Fabales	C_3	This study	N.A.
Argemone polyanthemos	Papaveraceae	Ranunculales	C_3	[91]	TRY
Aristida oligantha	Poaceae	Poales	C_4	[91]	TRY
Arnebia hispidissima	Boraginaceae	Boraginales	C_3	[190]	TRY
Artemisia scoparia	Asteraceae	Asterales	C_3	[96]	TRY
Arthraxon hispidus	Poaceae	Poales	C_4	[191]	N.A.
Aster subulatus	Asteraceae	Asterales	C_3	[91]	TRY
Astragalus coquimbensis	Fabaceae	Fabales	C_3	[190]	TRY
Avena barbata	Poaceae	Poales	C_3	[191]	N.A.
Avena fatua	Poaceae	Poales	C_3	[191]	N.A.
Avena sativa	Poaceae	Poales	C_3	[191]	N.A.
				This study	N.A.
Avena sterilis	Poaceae	Poales	C_3	This study	N.A.
Beckmannia syzigachne	Poaceae	Poales	C_3	[191]	N.A.
Bellardia trixago	Orobanchaceae	Lamiales	C_3	[190]	TRY
Bidens bipinnata	Asteraceae	Asterales	C_3	[91,190]	TRY
Bidens tinctoria	Asteraceae	Asterales	C_3	[101]	TRY
Borago officinalis	Boraginaceae	Boraginales	C_3	This study	N.A.
Bothriochloa pertusa	Poaceae	Poales	C_4	[27]	China Plant Trait
Brachiaria pubigera	Poaceae	Poales	C_4	[114]	TRY
Brachiaria reptans	Poaceae	Poales	C_4	[191]	N.A.
Brassica oleracea	Brassicaceae	Brassicales	C_3	This study	N.A.
Briza maxima	Poaceae	Poales	C_3	[191]	N.A.
Briza minor	Poaceae	Poales	C_3	[191]	N.A.
Bromus carinatus	Poaceae	Poales	C_3	[191]	N.A.
Bromus commutatus	Poaceae	Poales	C_3	[191]	N.A.
Bromus hordeaceus	Poaceae	Poales	C_3	[114]	TRY

				[191]	N.A.
Bromus japonicus	Poaceae	Poales	C_3	[191]	N.A.
Bromus rigidus	Poaceae	Poales	C_3	[191]	N.A.
Bromus rubens	Poaceae	Poales	C_3	[191]	N.A.
Bromus tectorum	Poaceae	Poales	C_3	[91,101]	TRY
				[191]	N.A.
Camelina microcarpa	Brassicaceae	Brassicales	C_3	[91]	TRY
Campanula americana	Campanulaceae	Asterales	C_3	[91]	TRY
Capsicum annuum	Solanaceae	Solanales	C_3	[190]	TRY
Carduus pycnocephalus	Asteraceae	Asterales	C_3	[118]	TRY
Catapodium rigidum	Poaceae	Poales	C_3	[191]	N.A.
Cenchrus echinatus	Poaceae	Poales	C_4	[191]	N.A.
Cenchrus longispinus	Poaceae	Poales	C_4	[91]	TRY
Cenchrus spinifex	Poaceae	Poales	C_4	[191]	N.A.
Centaurea solstitialis	Asteraceae	Asterales	C_3	[118]	TRY
Chaerophyllum procumbens	Apiaceae	Apiales	C_3	[91]	TRY
Chaetanthera limbata	Asteraceae	Asterales	C_3	[190]	TRY
Chamaecrista fasciculata	Fabaceae	Fabales	C_3	[91]	TRY
Chenopodiastrum simplex	Amaranthaceae	Caryophyllales	C_3	[91]	TRY
Chenopodium acuminatum	Amaranthaceae	Caryophyllales	C_3	[96,190]	TRY
Chenopodium fremontii	Amaranthaceae	Caryophyllales	C_3	[101]	TRY
Chenopodium vulvaria	Amaranthaceae	Caryophyllales	C_3	[101]	TRY
Chloris radiata	Poaceae	Poales	C_4	[191]	N.A.
Chloris virgata	Poaceae	Poales	C_3	[96,190]	TRY
				[191]	N.A.
Cicer arietinum	Fabaceae	Fabales	C_3	[192]	N.A.
Cicer reticulatum	Fabaceae	Fabales	C_3	[192]	N.A.
Coelachne japonica	Poaceae	Poales	C_3	[191]	N.A.
Coix lacryma-jobi	Poaceae	Poales	C_4	[191]	N.A.

Coldenia procumbens	Boraginaceae	Boraginales	C_3	[190]	TRY
Conium maculatum	Apiaceae	Apiales	C_3	[91]	TRY
Conobea multifida	Plantaginaceae	Lamiales	C_3	[91]	TRY
Corchorus tridens	Malvaceae	Malvales	C_3	[190]	TRY
Cosmos parviflorus	Asteraceae	Asterales	C_3	[101]	TRY
Croton capitatus	Euphorbiaceae	Malpighiales	C_3	[91]	TRY
Croton monanthogynus	Euphorbiaceae	Malpighiales	C_3	[91]	TRY
Cruckshanksia pumila	Rubiaceae	Gentianales	C_3	[190]	TRY
Cynosurus echinatus	Poaceae	Poales	C_3	[191]	N.A.
Cyperus acuminatus	Cyperaceae	Poales	C_3	[91]	TRY
Cyperus aquatilis	Cyperaceae	Poales	C_3	[190]	TRY
Cyperus leptocarpus	Cyperaceae	Poales	C_4	[190]	TRY
Dactyloctenium aegyptium	Poaceae	Poales	C_4	[190]	TRY
				[191]	N.A.
Dactyloctenium giganteum	Poaceae	Poales	C_4	[191]	N.A.
Dalea polygonoides	Fabaceae	Fabales	C_3	[101]	TRY
Damrongia clarkeana	Gesneriaceae	Lamiales	C_3	[27]	China Plant Trait
Desmodium brownii	Fabaceae	Fabales	C_3	[190]	TRY
Dicoma tomentosa	Asteraceae	Asterales	C_3	[190]	TRY
Digera muricata	Amaranthaceae	Caryophyllales	C_3	[190]	TRY
Digitaria bicornis	Poaceae	Poales	C_4	[114]	TRY
Digitaria ciliaris	Poaceae	Poales	C_4	[190]	TRY
				[191]	N.A.
Digitaria henryi	Poaceae	Poales	C_4	[191]	N.A.
Digitaria leptalea	Poaceae	Poales	C_4	[191]	N.A.
Digitaria radicosa	Poaceae	Poales	C_4	[191]	N.A.
Digitaria sanguinalis	Poaceae	Poales	C_4	[91]	TRY
Digitaria setigera	Poaceae	Poales	C_4	[190]	TRY
				[191]	N.A.

Digitaria violascens	Poaceae	Poales	C_4	190	TRY
				191	N.A.
Dimeria ornithopoda	Poaceae	Poales	C_4	191	N.A.
Dracocephalum moldavica	Lamiaceae	Lamiales	C_3	190	TRY
Drymaria molluginea	Caryophyllaceae	Caryophyllales	C_3	101	TRY
Dysphania aristata	Amaranthaceae	Caryophyllales	C_3	96	TRY
Echinochloa glabrescens	Poaceae	Poales	C_4	191	N.A.
Echinochloa muricata	Poaceae	Poales	C_4	91	TRY
Echinochloa oryzoides	Poaceae	Poales	C_4	191	N.A.
Eleusine coracana	Poaceae	Poales	C_4	191	N.A.
Eleusine indica	Poaceae	Poales	C_4	91	TRY
				191	N.A.
Ellisia nyctelea	Boraginaceae	Boraginales	C_3	91	TRY
Enneapogon polyphyllus	Poaceae	Poales	C_4	114	TRY
Eragrostis amabilis	Poaceae	Poales	C_4	190	TRY
Eragrostis arenicola	Poaceae	Poales	C_4	190	TRY
Eragrostis cilianensis	Poaceae	Poales	C_4	91,96	TRY
				191	N.A.
Eragrostis ciliaris	Poaceae	Poales	C_3	190	TRY
Eragrostis cummingii	Poaceae	Poales	C_4	114,190	TRY
				191	N.A.
Eragrostis mexicana	Poaceae	Poales	C_4	101	TRY
Eragrostis minor	Poaceae	Poales	C_4	96,190	TRY
				191	N.A.
Eragrostis multicaulis	Poaceae	Poales	C_3	190	TRY
				191	N.A.
Eragrostis pectinacea	Poaceae	Poales	C_4	91	TRY
Eragrostis pilosa	Poaceae	Poales	C_4	191	N.A.
Eragrostis tephrosanthos	Poaceae	Poales	C_4	190	TRY

Eriachne aristidea	Poaceae	Poales	C_4	[114]	TRY
Eriachne ciliata	Poaceae	Poales	C_4	[114]	TRY
Erigeron annuus	Asteraceae	Asterales	C_3	[91]	TRY
Erigeron philadelphicus	Asteraceae	Asterales	C_3	[91]	TRY
Erigeron strigosus	Asteraceae	Asterales	C_3	[91]	TRY
Eriocaulon sexangulare	Eriocaulaceae	Poales	C_3	[190]	TRY
Eriochloa contracta	Poaceae	Poales	C_4	[91]	TRY
Eriochloa procera	Poaceae	Poales	C_4	[191]	N.A.
Eriochloa villosa	Poaceae	Poales	C_4	[191]	N.A.
Eriogonum contiguum	Polygonaceae	Caryophyllales	C_3	[190]	TRY
Eriogonum pharnaceoides	Polygonaceae	Caryophyllales	C_3	[101]	TRY
Eruca vesicaria	Brassicaceae	Brassicales	C_3	[121]	TRY
Erythranthe glabrata	Phrymaceae	Lamiales	C_3	[91]	TRY
Euphorbia glanduligera	Euphorbiaceae	Malpighiales	C_3	[190]	TRY
Euphorbia glyptosperma	Euphorbiaceae	Malpighiales	C_4	[91]	TRY
Euphorbia humifusa	Euphorbiaceae	Malpighiales	C_4	[190]	TRY
Euphorbia maculata	Euphorbiaceae	Malpighiales	C_4	[91]	TRY
Euphorbia missurica	Euphorbiaceae	Malpighiales	C_4	[91]	TRY
Euphorbia nutans	Euphorbiaceae	Malpighiales	C_4	[91]	TRY
Euphorbia serpyllifolia	Euphorbiaceae	Malpighiales	C_3	[101]	TRY
Euphorbia spathulata	Euphorbiaceae	Malpighiales	C_3	[91]	TRY
Filago desertorum	Asteraceae	Asterales	C_3	[121]	TRY
Fimbristylis aestivalis	Cyperaceae	Poales	C_4	[190]	TRY
Geigeria alata	Asteraceae	Asterales	C_3	[190]	TRY
Geranium carolinianum	Geraniaceae	Geraniales	C_3	[91]	TRY
Gisekia africana	Gisekiaceae	Caryophyllales	C_3	[190]	TRY
Gisekia diffusa	Gisekiaceae	Caryophyllales	C_4	[190]	TRY
Grubovia dasyphylla	Amaranthaceae	Caryophyllales	C_3	[96]	TRY
Gutierrezia dracunculoides	Asteraceae	Asterales	C_3	[91]	TRY

Hainardia cylindrica	Poaceae	Poales	C_3	[191]	N.A.
Hedeoma hispida	Lamiaceae	Lamiales	C_3	[91]	TRY
Helianthus agrestis	Asteraceae	Asterales	C_3	[39]	BIEN
Helianthus annuus	Asteraceae	Asterales	C_3	[91]	TRY
				[39]	BIEN
Helianthus anomalus	Asteraceae	Asterales	C_3	[190]	TRY
Helianthus argophyllus	Asteraceae	Asterales	C_3	[39]	BIEN
Helianthus debilis	Asteraceae	Asterales	C_3	[39]	BIEN
Helianthus deserticola	Asteraceae	Asterales	C_3	[190]	TRY
Helianthus neglectus	Asteraceae	Asterales	C_3	[39]	BIEN
Helianthus praecox	Asteraceae	Asterales	C_3	[39]	BIEN
Hibiscus trionum	Malvaceae	Malvales	C_3	[91]	TRY
Hordeum distichon	Poaceae	Poales	C_3	[191]	N.A.
Hordeum murinum	Poaceae	Poales	C_3	[191]	N.A.
Hordeum pusillum	Poaceae	Poales	C_3	[91]	TRY
Hordeum spontaneum	Poaceae	Poales	C_3	[191]	N.A.
Hordeum vulgare	Poaceae	Poales	C_3	[191]	N.A.
Hypericum gramineum	Hypericaceae	Malpighiales	C_3	[124]	AusTraits
Hypertelis cerviana	Molluginaceae	Caryophyllales	C_4	[190]	TRY
Impatiens furcillata	Balsaminaceae	Ericales	C_3	[96]	TRY
				[27]	China Plant Trait
Incarvillea sinensis	Bignoniaceae	Lamiales	C_3	[190]	TRY
Indigofera astragalina	Fabaceae	Fabales	C_3	[190]	TRY
Indigofera cordifolia	Fabaceae	Fabales	C_3	[190]	TRY
Isachne globosa	Poaceae	Poales	C_3	[190]	TRY
				[191]	N.A.
Isachne lutchuensis	Poaceae	Poales	C_3	[191]	N.A.
Isachne nipponensis	Poaceae	Poales	C_3	[191]	N.A.
Iva annua	Asteraceae	Asterales	C_3	[91]	TRY

Ixeris chinensis	Asteraceae	Asterales	C_3	[96]	TRY
				[27]	China Plant Trait
Justicia debilis	Acanthaceae	Lamiales	C_3	[190]	TRY
Justicia procumbens	Acanthaceae	Lamiales	C_3	[190]	TRY
Kali collinum	Amaranthaceae	Caryophyllales	C_4	[96,190]	TRY
Kalimeris altaica	Asteraceae	Asterales	C_3	[96,190]	TRY
Kaokochloa nigrirostris	Poaceae	Poales	C_4	[190]	TRY
Koelpinia linearis	Asteraceae	Asterales	C_3	[121]	TRY
Krigia caespitosa	Asteraceae	Asterales	C_3	[91]	TRY
Kummerowia striata	Fabaceae	Fabales	C_3	[96]	TRY
Lachnagrostis filiformis	Poaceae	Poales	C_3	[191]	N.A.
Lactuca canadensis	Asteraceae	Asterales	C_3	[91]	TRY
Lactuca ludoviciana	Asteraceae	Asterales	C_3	[91]	TRY
Lactuca saligna	Asteraceae	Asterales	C_3	[91]	TRY
Lactuca sativa	Asteraceae	Asterales	C_3	This study	N.A.
Lactuca serriola	Asteraceae	Asterales	C_3	[91]	TRY
				This study	N.A.
Laennecia schiedeana	Asteraceae	Asterales	C_3	[101]	TRY
Lagurus ovatus	Poaceae	Poales	C_3	[191]	N.A.
Laportea canadensis	Urticaceae	Rosales	C_3	[91]	TRY
Lepidium densiflorum	Brassicaceae	Brassicales	C_3	[91,101]	TRY
Leptochloa fusca	Poaceae	Poales	C_3	[91,114]	TRY
				[191]	N.A.
Leptochloa panicea	Poaceae	Poales	C_4	[191]	N.A.
Leucas urticifolia	Lamiaceae	Lamiales	C_3	[190]	TRY
Leucheria cummingii	Asteraceae	Asterales	C_3	[190]	TRY
Linum australe	Linaceae	Malpighiales	C_3	[101]	TRY
Linum stelleroides	Linaceae	Malpighiales	C_3	[190]	TRY
Linum sulcatum	Linaceae	Malpighiales	C_3	[91]	TRY

Lobelia chevalieri	Campanulaceae	Asterales	C_3	190	TRY
Lolium rigidum	Poaceae	Poales	C_3	191	N.A.
Lotus corniculatus	Fabaceae	Fabales	C_3	132	TRY
Lupinus kingii	Fabaceae	Fabales	C_3	101	TRY
Malesherbia multiflora	Passifloraceae	Malpighiales	C_3	190	TRY
Malvastrum hispidum	Malvaceae	Malvales	C_3	91	TRY
Melanocenchris jacquemontii	Poaceae	Poales	C_4	190	TRY
Melinis repens	Poaceae	Poales	C_4	190	TRY
Microstegium fasciculatum	Poaceae	Poales	C_4	191	N.A.
Microstegium japonicum	Poaceae	Poales	C_4	191	N.A.
Microstegium nudum	Poaceae	Poales	C_4	191	N.A.
Microstegium vimineum	Poaceae	Poales	C_4	191	N.A.
Mollugo verticillata	Molluginaceae	Caryophyllales	C_3	91,190	TRY
Muhlenbergia minutissima	Poaceae	Poales	C_4	101	TRY
Muhlenbergia ramulosa	Poaceae	Poales	C_4	101	TRY
Myosotis verna	Boraginaceae	Boraginales	C_3	91	TRY
Nama dichotoma	Boraginaceae	Boraginales	C_3	101	TRY
Nolana aplocaryoides	Solanaceae	Solanales	C_3	190	TRY
Nolana elegans	Solanaceae	Solanales	C_3	190	TRY
Notoceras bicorne	Brassicaceae	Brassicales	C_3	121	TRY
Oenothera curtiflora	Onagraceae	Myrtales	C_3	91	TRY
Oenothera filiformis	Onagraceae	Myrtales	C_3	91	TRY
Oenothera nana	Onagraceae	Myrtales	C_3	190	TRY
Oldenlandia herbacea	Rubiaceae	Gentianales	C_3	190	TRY
Oligochaeta ramosa	Asteraceae	Asterales	C_3	190	TRY
Oplismenus burmanni	Poaceae	Poales	C_3	191	N.A.
Oryza sativa	Poaceae	Poales	C_3	191	N.A.
Oxybasis glauca	Amaranthaceae	Caryophyllales	C_3	96	TRY
Panicum bisulcatum	Poaceae	Poales	C_3	191	N.A.

				[193]	AusTraits
Panicum capillare	Poaceae	Poales	C_4	[91]	TRY
				[191]	N.A.
Panicum dichotomiflorum	Poaceae	Poales	C_4	[91]	TRY
				[191]	N.A.
Panicum flexuosum	Poaceae	Poales	C_4	[27]	China Plant Trait
Panicum laevinode	Poaceae	Poales	C_4	[193]	AusTraits
Panicum miliaceum	Poaceae	Poales	C_4	[190]	TRY
				[191]	N.A.
Panicum mindanaense	Poaceae	Poales	C_4	[193]	AusTraits
Panicum trachyrhachis	Poaceae	Poales	C_4	[193]	AusTraits
Panicum verrucosum	Poaceae	Poales	C_4	[191]	N.A.
Parietaria pensylvanica	Urticaceae	Rosales	C_3	[91]	TRY
Paronychia arabica	Caryophyllaceae	Caryophyllales	C_3	[121]	TRY
Pennisetum glaucum	Poaceae	Poales	C_4	[190]	TRY
				[191]	N.A.
				This study	N.A.
Perilla frutescens	Lamiaceae	Lamiales	C_3	[190]	TRY
Perityle emoryi	Asteraceae	Asterales	C_3	[190]	TRY
Perotis patens	Poaceae	Poales	C_4	[114]	TRY
Persicaria bungeana	Polygonaceae	Caryophyllales	C_3	[91]	TRY
Persicaria maculosa	Polygonaceae	Caryophyllales	C_3	[91]	TRY
Phalaris canariensis	Poaceae	Poales	C_3	[191]	N.A.
Phalaris minor	Poaceae	Poales	C_3	[191]	N.A.
Phalaris paradoxa	Poaceae	Poales	C_3	[191]	N.A.
Phaseolus vulgaris	Fabaceae	Fabales	C_3	[54]	TRY
Phleum paniculatum	Poaceae	Poales	C_3	[191]	N.A.
Phoebanthus tenuifolius	Asteraceae	Asterales	C_3	[39]	BIEN
Phyllanthus maderaspatensis	Phyllanthaceae	Malpighiales	C_3	[190]	TRY

Pilea pumila	Urticaceae	Rosales	C_3	[91]	TRY
Plantago argyrea	Plantaginaceae	Lamiales	C_3	[101]	TRY
Plantago aristata	Plantaginaceae	Lamiales	C_3	[91]	TRY
Plantago ciliata	Plantaginaceae	Lamiales	C_3	[121]	TRY
Plantago litorea	Plantaginaceae	Lamiales	C_3	[190]	TRY
Plantago ovata	Plantaginaceae	Lamiales	C_3	[121]	TRY
Plantago patagonica	Plantaginaceae	Lamiales	C_3	[91]	TRY
Plantago rhodosperma	Plantaginaceae	Lamiales	C_3	[91]	TRY
Plantago virginica	Plantaginaceae	Lamiales	C_3	[91]	TRY
Poa annua	Poaceae	Poales	C_3	[190]	TRY
				[191]	N.A.
Poa crassinervis	Poaceae	Poales	C_3	[191]	N.A.
Poa hisauchii	Poaceae	Poales	C_3	[191]	N.A.
Poa nepalensis	Poaceae	Poales	C_3	[191]	N.A.
Polycarpaea corymbosa	Caryophyllaceae	Caryophyllales	C_4	[190]	TRY
Polygonum aviculare	Polygonaceae	Caryophyllales	C_3	[91,101]	TRY
Polygonum douglasii	Polygonaceae	Caryophyllales	C_3	[101]	TRY
Polygonum ramosissimum	Polygonaceae	Caryophyllales	C_3	[91]	TRY
Polygonum tenue	Polygonaceae	Caryophyllales	C_3	[91]	TRY
Polypogon fugax	Poaceae	Poales	C_3	[191]	N.A.
Polypogon monspeliensis	Poaceae	Poales	C_3	[191]	N.A.
Portulaca bicolor	Portulacaceae	Caryophyllales	C_3	[190]	TRY
Pseudognaphalium obtusifolium	Asteraceae	Asterales	C_3	[91]	TRY
Rostraria cristata	Poaceae	Poales	C_3	[114]	TRY
				[191]	N.A.
Rottboellia cochinchinensis	Poaceae	Poales	C_4	[191]	N.A.
Rudbeckia amplexicaulis	Asteraceae	Asterales	C_3	[91]	TRY
Sacciolepis indica	Poaceae	Poales	C_3	[191]	N.A.
				[190]	TRY

Salomonia cantoniensis	Polygalaceae	Fabales	C_3	[190]	TRY
Schismus barbatus	Poaceae	Poales	C_3	[121]	TRY
Schizachyrium brevifolium	Poaceae	Poales	C_4	[191]	N.A.
Schizachyrium crinizonatum	Poaceae	Poales	C_4	[114]	TRY
Schizanthus laetus	Solanaceae	Solanales	C_3	[190]	TRY
Secale cereale	Poaceae	Poales	C_3	[191]	N.A.
Senecio carnosulus	Asteraceae	Asterales	C_3	[190]	TRY
Sesamum indicum	Pedaliaceae	Lamiales	C_3	This study	N.A.
Sesamum schinzianum	Pedaliaceae	Lamiales	C_3	[190]	TRY
Setaria barbata	Poaceae	Poales	C_4	[191]	N.A.
Setaria faberi	Poaceae	Poales	C_4	[191]	N.A.
Setaria helvola	Poaceae	Poales	C_4	[91,190]	TRY
				[191]	N.A.
Setaria italica	Poaceae	Poales	C_4	[190]	TRY
				[191]	N.A.
Setaria plicata	Poaceae	Poales	C_3	[27]	China Plant Trait
Setaria verticillata	Poaceae	Poales	C_4	[191]	N.A.
Setaria viridis	Poaceae	Poales	C_4	[91,96,190]	TRY
				[191]	N.A.
Sicyos angulatus	Cucurbitaceae	Cucurbitales	C_3	[91]	TRY
Silene antirrhina	Caryophyllaceae	Caryophyllales	C_3	[91]	TRY
Solanum lycopersicum	Solanaceae	Solanales	C_3	This study	N.A.
Solanum pimpinellifolium	Solanaceae	Solanales	C_3	This study	N.A.
Solanum ptychanthum	Solanaceae	Solanales	C_3	[91]	TRY
Solanum rostratum	Solanaceae	Solanales	C_3	[91]	TRY
Sonchus asper	Asteraceae	Asterales	C_3	[91]	TRY
Sorghum bicolor	Poaceae	Poales	C_4	[191]	N.A.
				[194]	AusTraits
Sorghum intrans	Poaceae	Poales	C_4	[114]	TRY

Spergularia diandra	Caryophyllaceae	Caryophyllales	C_3	[121]	TRY
Sphenopholis obtusata	Poaceae	Poales	C_3	[91]	TRY
Sporobolus fertilis	Poaceae	Poales	C_4	[191]	N.A.
Sporobolus piliferus	Poaceae	Poales	C_4	[191]	N.A.
Stipa capensis	Poaceae	Poales	C_3	[121]	TRY
Stipagrostis namibensis	Poaceae	Poales	C_4	[190]	TRY
Stipagrostis subacaulis	Poaceae	Poales	C_4	[190]	TRY
Streptoglossa cylindriceps	Asteraceae	Asterales	C_3	[124]	AusTraits
Suaeda glauca	Amaranthaceae	Caryophyllales	C_3	[96,190]	TRY
Tephrosia capillipes	Fabaceae	Fabales	C_3	[190]	TRY
Teucrium canadense	Lamiaceae	Lamiales	C_3	[91]	TRY
Torilis arvensis	Apiaceae	Apiales	C_3	[91]	TRY
Tragus racemosus	Poaceae	Poales	C_4	[96,190]	TRY
				[191]	N.A.
Tribulus pentandrus	Zygophyllaceae	Zygophyllales	C_4	[190]	TRY
Tribulus terrestris	Zygophyllaceae	Zygophyllales	C_4	[91,96,190]	TRY
				[27]	China Plant Trait
Trifolium repens	Fabaceae	Fabales	C_3	[91,190]	TRY
Trigastrotheca pentaphylla	Molluginaceae	Caryophyllales	C_3	[190]	TRY
Trigonella officinalis	Fabaceae	Fabales	C_3	[91]	TRY
Triodanis leptocarpa	Campanulaceae	Asterales	C_3	[91]	TRY
Triticum aestivum	Poaceae	Poales	C_3	[191]	N.A.
Vicia faba	Fabaceae	Fabales	C_3	This study	N.A.
Vicia narbonensis	Fabaceae	Fabales	C_3	This study	N.A.
Viola polypoda	Violaceae	Malpighiales	C_3	[190]	TRY
Viola pusilla	Violaceae	Malpighiales	C_3	[190]	TRY
Vulpia bromoides	Poaceae	Poales	C_3	[191]	N.A.
Vulpia myuros	Poaceae	Poales	C_3	[191]	N.A.
Vulpia octoflora	Poaceae	Poales	C_3	[191]	N.A.

Whiteochloa multiciliata	Poaceae	Poales	C_4	[114]	TRY
Xanthisma gracile	Asteraceae	Asterales	C_3	[101]	TRY
Xanthium strumarium	Asteraceae	Asterales	C_3	[91,190]	TRY
Zea luxurians	Poaceae	Poales	C_4	[190]	TRY
Zea mays	Poaceae	Poales	C_4	[191]	N.A.

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Table S6. List of crop accessions used in the *experimental dataset*. Common and botanical names, family, photosynthetic pathway, domestication status, and seed origin information for each accession of the 11 crops used in the experiment. Accession identifier refers to the code assigned by each seed donor, with the exception of commercial companies (N.A. = not applicable). Accession country refers to the country where seeds were originally collected, if applicable. Seed donor (CGN: Center for Genetic Resources, The Netherlands; CITA: Centro de Investigación y Transferencia Agroalimentaria de Aragón, Spain; COMAV: Instituto Universitario de Conservación y Mejora de la Agrodiversidad Valenciana, Spain; CRF: Centro Nacional de Recursos Fitogenéticos-INIA, Spain; ICARDA: International Center for Agricultural Research in Dry Areas, Syria; IPK: Germplasm bank of the Leibniz Institute of Plant Genetics and Crop Plant Research, Germany; NPGS: National Plant Germplasm System-USDA, U.S.A.; *: commercial company).

Common name	Family	Photosynthetic pathway	Botanical name	Domestication status	Accession identifier	Accession country	Seed donor
Amaranth	Amaranthaceae	C_4	*Amaranthus hybridus* L.	Wild	PI 500234	Zambia	NPGS
					PI 652417	Brazil	NPGS
			Amaranthus cruentus L.	Landrace	Ames 2001	Ghana	NPGS
					PI 643050	Mexico	NPGS
				Improved	AMA 169	Nepal	IPK
					Ames 15197	Argentina	NPGS
Borago	Boraginaceae	C_3	*Borago officinalis* L.	Wild	BGHZ5329	Spain	CITA
					BGHZ4294	Spain	CITA
				Landrace	BGHZ0363	Spain	CITA
					BGHZ2340	Spain	CITA
				Improved	N.A.	N.A.	Battle*
					N.A.	N.A.	Rocalba*
Cabbage	Brassicaceae	C_3	*Brassica oleracea* L.	Wild	CGN06903	France	CGN
					CGN18947	Germany	CGN
				Landrace	CGN14079	Belgium	CGN
					CGN15773	Portugal	CGN
				Improved	N.A.	N.A.	Rocalba*

					N.A.	N.A.	Battle*
Faba bean	Fabaceae	C_3	*Vicia narbonensis* L.	Wild	IG 111590 IFVI 5266	Tunisia	ICARDA
					BGE031092	Spain	CRF
			Vicia faba L.	Landrace	BGE022388	Spain	CRF
					BGE031076	Spain	CRF
				Improved	N.A.	N.A.	Rocalba*
					N.A.	N.A.	Battle*
Lettuce	Asteraceae	C_3	*Lactuca serriola* L.	Wild	BGE034705	Spain	CRF
					LAC 1079	Italy	IPK
			Lactuca sativa L.	Landrace	BGV003526	Spain	COMAV
					BGV001094	Spain	COMAV
				Improved	N.A.	N.A.	Battle*
					BGV005752	Spain	COMAV
Millet	Poaceae	C_4	*Cenchrus americanus* (L.) Morrone	Wild	PI 537068	Niger	NPGS
					PEN 1028	Yemen	IPK
				Landrace	PEN 837	Tunisia	IPK
					PEN 687	Libya	IPK
				Improved	PI 586660	Burkina Faso	NPGS
					PEN 1257	Soviet Union	IPK
Oat	Poaceae	C_3	*Avena sterilis* L.	Wild	BGE049079	Spain	CRF
					IG 100379 IFMI 3096	Turkey	ICARDA
			Avena sativa L.	Landrace	BGE008136	Spain	CRF
					BGE008166	Spain	CRF
				Improved	N.A.	N.A.	Battle*
					BGE024681	Spain	CRF
Okra	Malvaceae	C_3	*Abelmoschus tuberculatus* Pal & Singh	Wild	PI 639676	Sri Lanka	NPGS
					PI 639681	India	NPGS
			Abelmoschus esculentus (L.) Moench	Landrace	PI 489782	Ivory Coast	NPGS
					PI 505564	Zambia	NPGS
				Improved	N.A.	N.A.	Battle*
					PI 548700	India	NPGS

Peanut	Fabaceae	C_3	*Arachis monticola* Krapov. & Rigoni	Wild	PI 263393	Brazil	NPGS
					PI 468196	Argentina	NPGS
			Arachis hypogaea L.	Landrace	PI 602352	Brazil	NPGS
					Grif 373	Sudan	NPGS
				Improved	PI 538758	Burkina Faso	NPGS
					PI 550688	China	NPGS
Sesamum	Pedaliaceae	C_3	*Sesamum indicum* L.	Wild	SESA 17	Yemen	IPK
					SESA 20	Yemen	IPK
				Landrace	SESA 4	North Korea	IPK
					SESA 5	Irak	IPK
				Improved	N.A.	N.A.	Rocalba*
					SESA 14	N.A.	IPK
Tomato	Solanaceae	C_3	*Solanum pimpinellifolium* L.	Wild	BGV007948	Peru	COMAV
					LYC 1	N.A.	IPK
			Solanum lycopersicum L.	Landrace	LYC 15	Switzerland	IPK
					LYC 1014	Guatemala	IPK
				Improved	N.A.	N.A.	Battle*
					N.A.	N.A.	Clause*

Fig. S1. Univariate comparisons between domesticates *vs*. wild species that were never domesticated in the ecophysiological traits. Domesticates (D) are shown in orange and wild annual herbs (W) in green. Symbols indicate photosynthetic pathway: C_3 (circles) *vs*. C_4 (triangles). Points are trait mean of species grouped according to their botanical order. Statistical differences were evaluated from phylogenetic generalized least squares (PGLS) models across 1000 randomly resolved trees and asterisks denote the mean *P*-value (., $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Total sample size is shown for each trait, plant type (D *vs*. W) and photosynthetic pathway. Abbreviations: A_{area}, net photosynthetic rate per unit area; g_{wv}, stomatal conductance to water vapour; [N_{mass}], mass-based leaf N concentration; SLA, specific leaf area; and $\delta^{13}C$, ^{13}C isotopic composition.

Fig. S2. Trait correlations. Correlations among $\log_{10}$-transformed ecophysiological traits plotted separately for photosynthetic pathway (C_3 *vs*. C_4). Solid lines represent the fitted phylogenetic generalised least squares (PGLS) model and were drawn when trait correlation was significant. PGLS models included one ecophysiological trait as response variable and the interaction between another ecophysiological trait and photosynthetic pathway as fixed effects. Abbreviations: A_{area}, net photosynthetic rate per unit area; g_{wv}, stomatal conductance to water vapour; [N_{mass}], mass-based leaf N concentration; SLA, specific leaf area; and $\delta^{13}C$, ^{13}C isotopic composition.

Fig. S3. Effect-size of domestication and improvement. Effect-size of domestication (landrace-progenitor comparations) and improvement (improved-landrace comparations) on the five studied ecophysiological traits: net photosynthetic rate per unit area (a), stomatal conductance to water vapour (b), leaf N concentration (c), specific leaf area (d), and ^{13}C isotopic composition (e), for the *experimental dataset*. The circles show the effect-size estimated by Hedges´*G* and 95% confidence intervals. Negative scores of Hedges' *G* indicate negative effects of domestication or improvement on the ecophysiological traits.

Fig. S4. Results of principal components analysis for mass-based leaf N concentration ([N_{mass}]) and ^{13}C isotopic composition ($\delta^{13}C$). Ellipses represent 95% confidence areas for domesticates (orange) and wild species (green). Centroids are represented by the largest point of the same colour, while the smaller points represent

individual species. Axes percentages represent the amount of variation accounted for by each principal component.

Fig. S1

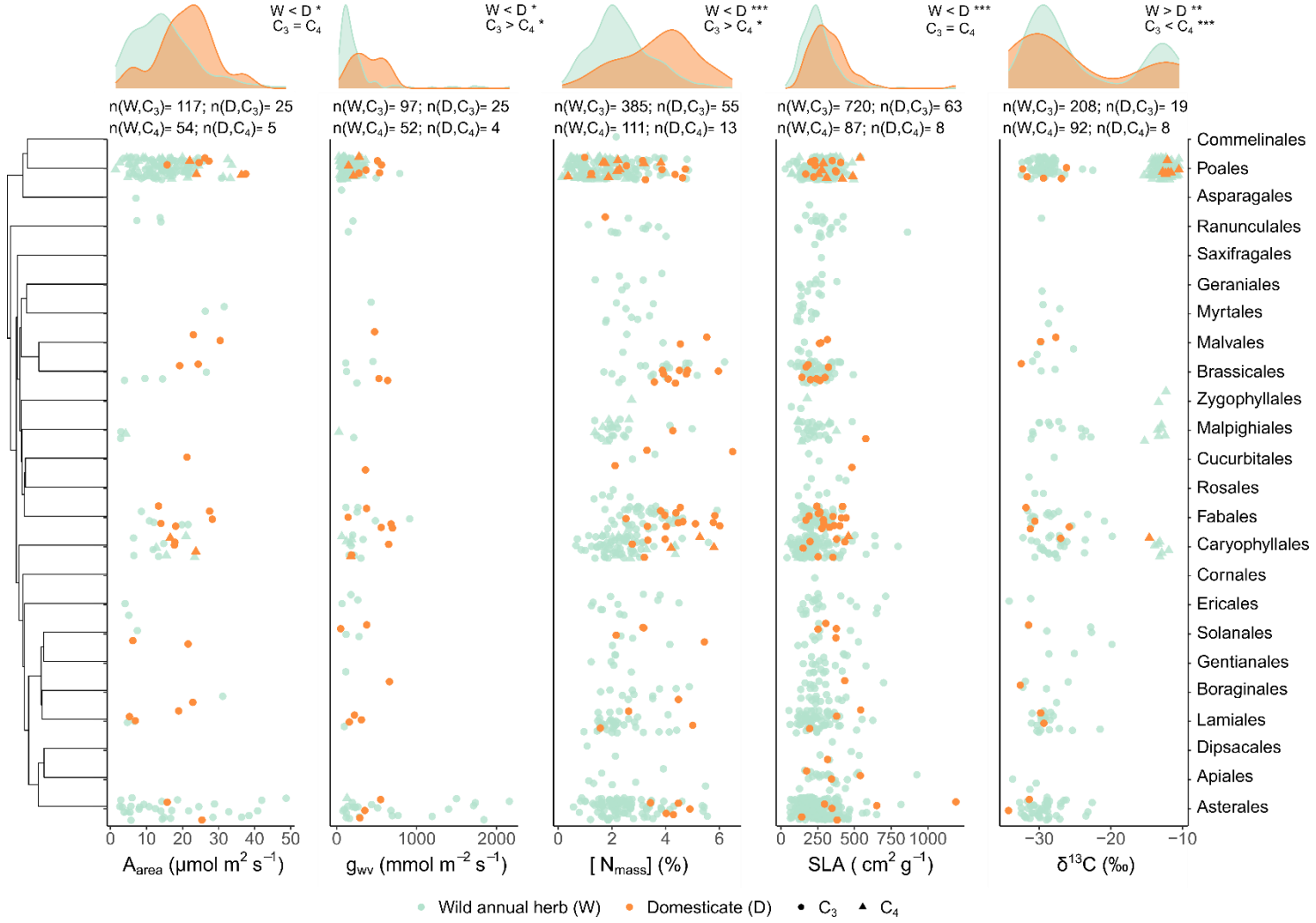

W < D *
C3 = C4
W < D *
C3 > C4 *
W < D ***
C3 > C4 *
W < D ***
C3 = C4
W > D **
C3 < C4 ***
n(W,C3)= 117; n(D,C3)= 25
n(W,C4)= 54; n(D,C4)= 5
n(W,C3)= 97; n(D,C3)= 25
n(W,C4)= 52; n(D,C4)= 4
n(W,C3)= 385; n(D,C3)= 55
n(W,C4)= 111; n(D,C4)= 13
n(W,C3)= 720; n(D,C3)= 63
n(W,C4)= 87; n(D,C4)= 8
n(W,C3)= 208; n(D,C3)= 19
n(W,C4)= 92; n(D,C4)= 8
Commelinales
Poales
Asparagales
Ranunculales
Saxifragales
Geraniales
Myrtales
Malvales
Brassicales
Zygophyllales
Malpighiales
Cucurbitales
Rosales
Fabales
Caryophyllales
Cornales
Ericales
Solanales
Gentianales
Boraginales
Lamiales
Dipsacales
Apiales
Asterales
0 10 20 30 40 50
Aarea (μmol m2 s−1)
0 1000 2000
gwv (mmol m−2 s−1)
0 2 4 6
[Nmass] (%)
0 250 500 750 1000
SLA (cm2 g−1)
−30 −20 −10
δ13C (‰)
Wild annual herb (W)
Domesticate (D)
C3
C4

Fig. S2

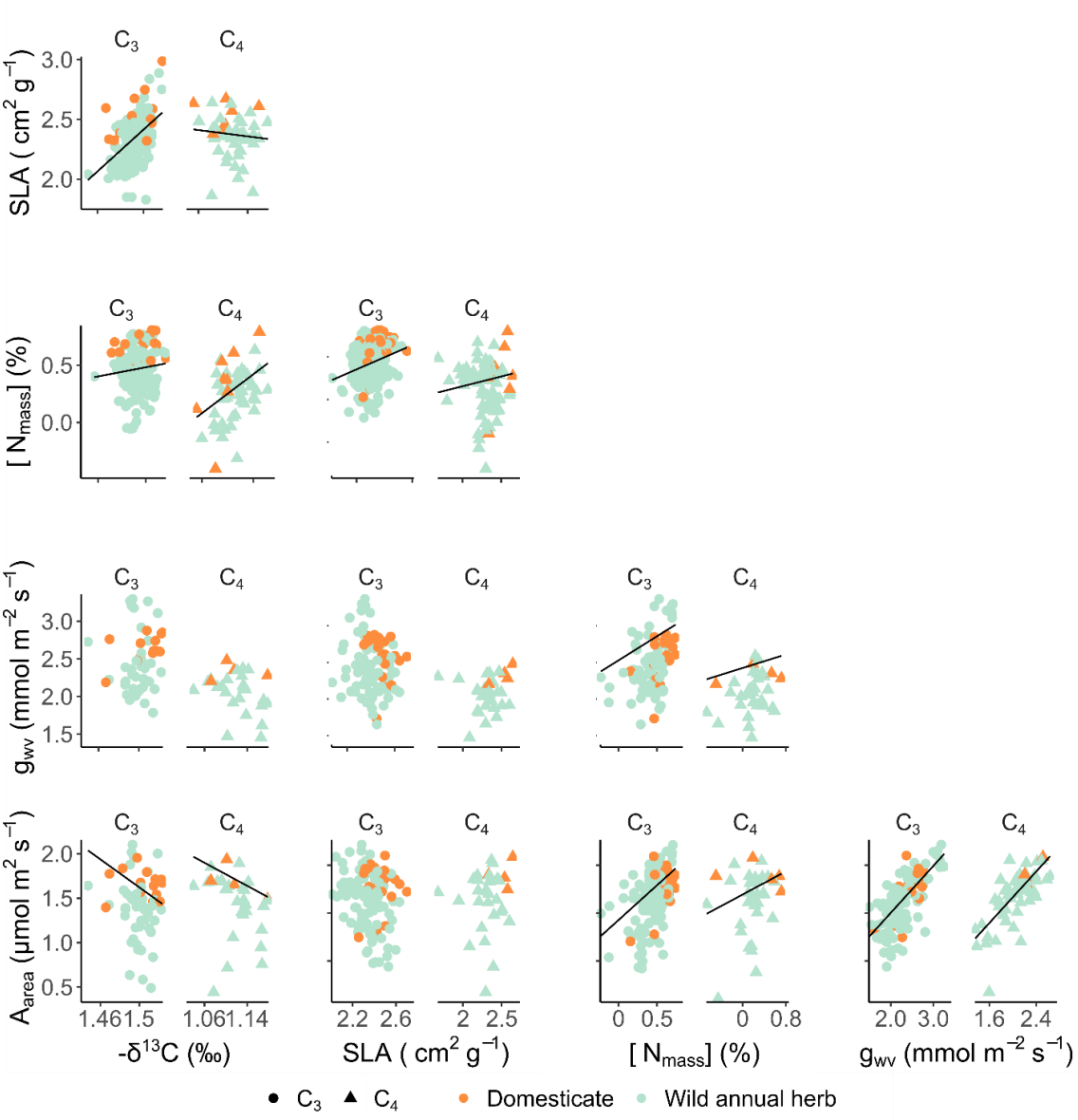

C3
C4
SLA (cm2 g−1)
[Nmass] (%)
gwv (mmol m−2 s−1)
Aarea (μmol m2 s−1)
-δ13C (‰)
SLA (cm2 g−1)
[Nmass] (%)
gwv (mmol m−2 s−1)
Domesticate
Wild annual herb

Fig. S3

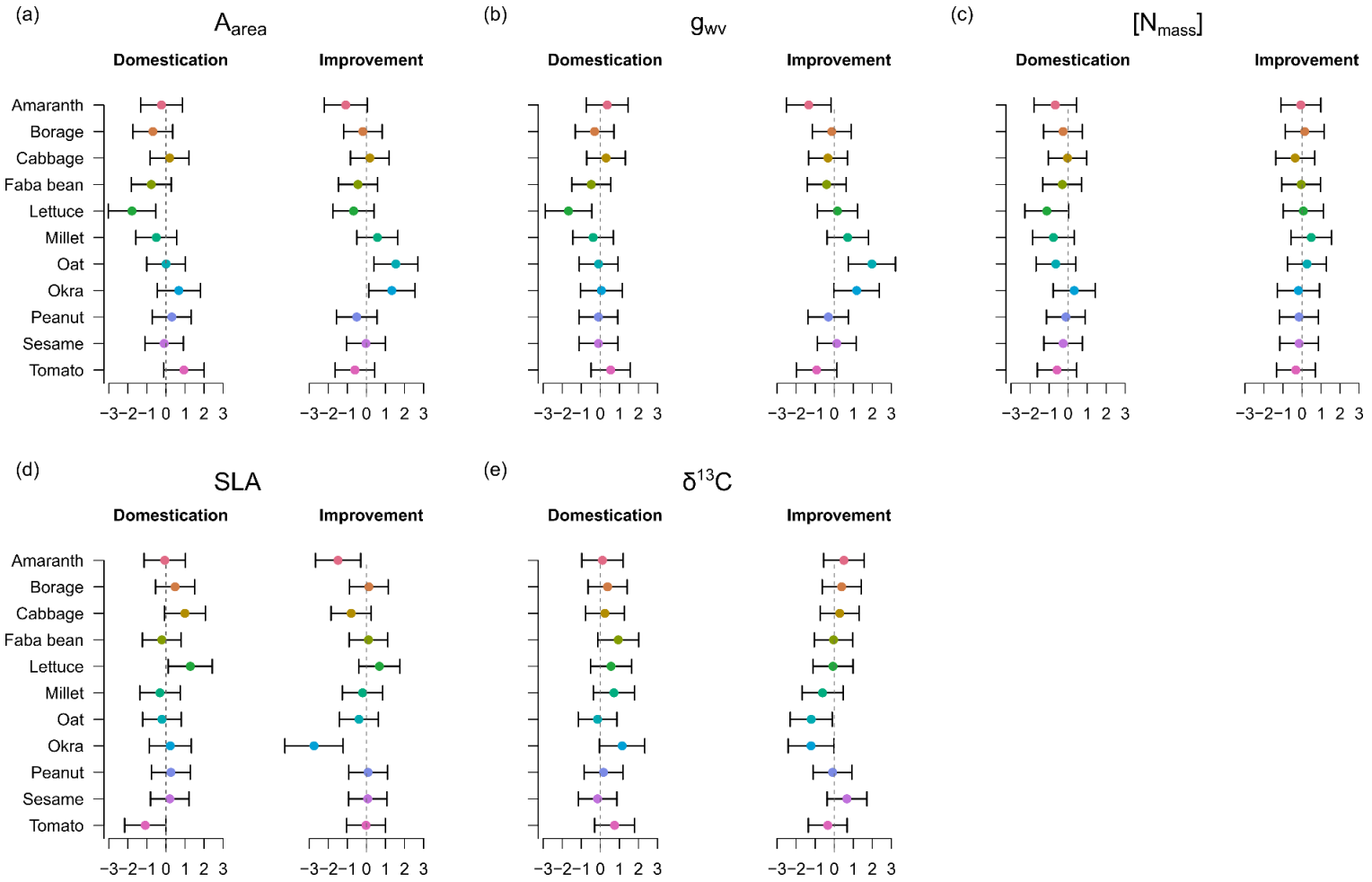
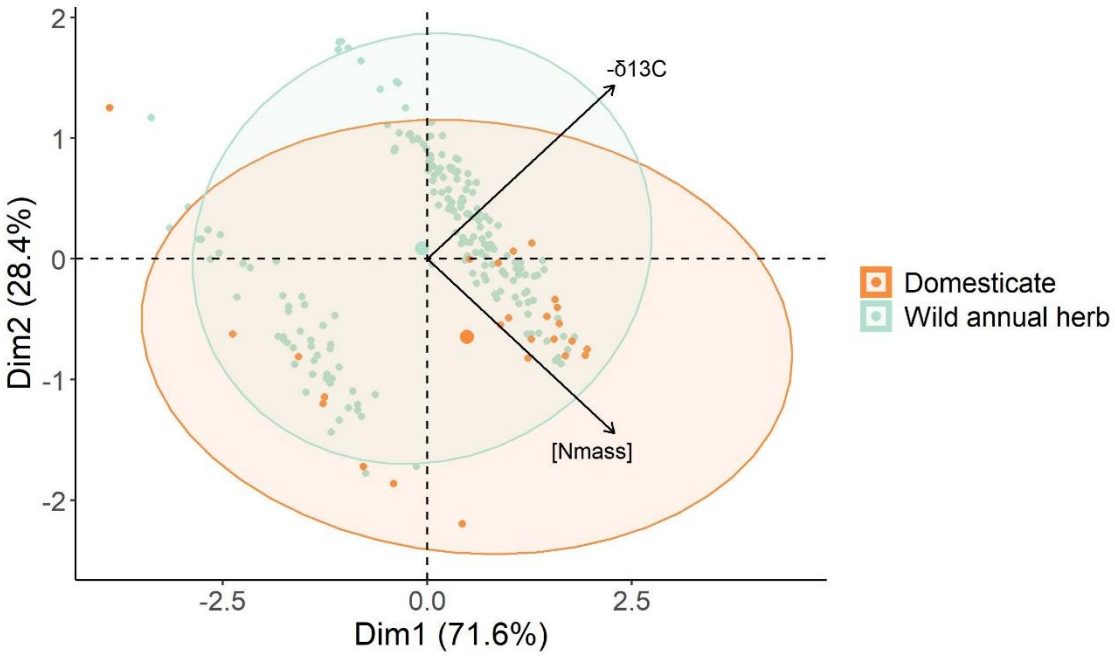

(a)
A_{area}
(b)
g_{wv}
(c)
$[N_{mass}]$
(d)
SLA
(e)
$\delta^{13}C$
Domestication
Improvement
Amaranth
Borage
Cabbage
Faba bean
Lettuce
Millet
Oat
Okra
Peanut
Sesame
Tomato
−3 −2 −1 0 1 2 3

Fig. S4


2
1
0
-1
-2
Dim2 (28.4%)
-2.5
0.0
2.5
Dim1 (71.6%)
-δ13C
[Nmass]
Domesticate
Wild annual herb

CHAPTER 2

Disparities among crop species in the evolution of growth rates: the role of distinct origins and domestication histories

Alicia Gómez-Fernández, Colin P. Osborne, Mark Rees, Javier Palomino, Carlos Ingala, Guillermo Gómez and Rubén Milla

Manuscript published in *New Phytologist*

ABSTRACT

Growth rates vary widely among plants with different strategies. For crops, evolution under predictable and high-resource environments might favour rapid resource acquisition and growth, but whether this strategy consistently evolved during domestication and improvement remains unclear. Here, we report a comprehensive study of the evolution of growth rates based on comparisons among wild, landrace, and improved accessions of 19 herbaceous crops grown under common conditions. We also examined the underlying growth components and the influence of crop origin and history on growth evolution. Domestication and improvement did not affect growth consistently, *i.e*. growth rates increased or decreased or remained unchanged in different crops. Crops selected for fruits increased the physiological component of growth (net assimilation rate), whereas leaf and seed crops showed larger domestication effects on morphology (leaf mass ratio and specific leaf area). Moreover, climate and phylogeny contributed to explaining the effects of domestication and changes in growth. Crop-specific responses to domestication and improvement suggest that selection for high yield has not consistently changed growth rates. The trade-offs between morpho-physiological traits and the distinct origins and histories of crops accounted for the variability in growth changes. These findings have far-reaching implications for our understanding of crop performance and adaptation.

INTRODUCTION

Evolution under cultivation involves a diverse range of natural and artificial selection pressures that have changed crop phenotypes for millennia (Evans, 1993; Doebley *et al.*, 2006; Purugganan & Fuller, 2009). Our understanding of crop evolution is primarily based on reproductive traits (*e.g.* seed size, flowering time, yield), which have received more attention than vegetative development and growth (Milla *et al.*, 2015; Wood *et al.*, 2015; Martin & Isaac, 2018). In resource-rich, predictable systems, growth rates tend to be fast, leading to the assumption that crops may have evolved towards a rapid, acquisitive trait profile (Aerts & Chapin, 1999; Craine, 2009; Milla *et al.*, 2015). Despite the increasing number of studies addressing domestication from an eco-evolutionary perspective or a trait-based approach (*e.g.* Blesh, 2018; Martin *et al.*, 2018; Roucou *et al.*, 2018; Chacón-Labella *et al.*, 2019; Preece *et al.*, 2021), there is a lack of comparative work assessing the evolution of growth dynamics in cultivation.

Crops are generally larger than their wild progenitors (Preece *et al.*, 2016; Milla & Matesanz, 2017) and invest less in chemical and physical defences (Meyer *et al.*, 2012; Chen *et al.*, 2015; Simpson *et al.*, 2017). Increased resource allocation to harvestable organs and earlier and more synchronous flowering and maturation phenologies are typical of crops (Meyer & Purugganan, 2013). In addition, some herbaceous crops have higher photosynthetic rates and leaf nitrogen concentrations than their wild progenitors (Delgado-Baquerizo *et al.*, 2016; Roucou *et al.*, 2017; Nadal & Flexas, 2018). However, the effects of domestication on growth rates appear to be inconsistent or variable across crops. For example, modern cereals and other crop species show no increase in growth rates during domestication (Gifford & Evans, 1981). These results have recently been supported by other studies on a number of cereal and legume species, which found no overall effect of domestication on growth rates (Preece *et al.*, 2016; Simpson *et al.*, 2017).

Why previous work has reported idiosyncratic growth responses to domestication may be due in part to the properties of the most common metric of growth, relative growth rate (RGR), and the methods used to measure it. RGR, defined as the rate of biomass increase relative to the biomass of the plant at the beginning of a given time interval, is the product of a physiological (net assimilation rate, NAR), a biomass allocation (leaf mass ratio, LMR), and a morphological component (specific leaf area, SLA; Poorter,

1990). Given the mathematical relationships among these traits, changes in RGR depend not only on variation in its components but also on how they co-vary with each other (see Supporting Information Table S1 for a list of abbreviations and a diagram of the mathematical relationships among growth traits). For example, a change in NAR will result in a change in RGR unless NAR co-varies negatively with LMR and/or SLA. Empirical studies of plant domestication often report changes in physiology, biomass allocation, and leaf morphology in opposite directions and in inconsistent ways. For example, SLA is lower in wild progenitors of several crops, whereas leaf/stem fraction is higher compared to domesticates (Milla & Matesanz, 2017). Alternatively, leaf photosynthetic rate (*i.e.* an instantaneous proxy for NAR) is higher in modern soybean, while SLA is lower than in its wild progenitors (Togashi & Oikawa, 2021). Therefore, RGR might not differ between crops and their progenitors because domestication has exerted opposite effects on its underlying components.

Another confounding effect may arise from the fact that RGR tends to decrease as plants grow larger through increased investment in structural components, self-shading and tissue turnover (Evans, 1972; Grime & Hunt, 1975). The larger size of domesticated crops compared to their wild progenitors could therefore mask a faster growth rate at a given size and have compromised the accuracy of previous work (Turnbull *et al.*, 2008; Rose *et al.*, 2009). In addition, the methods used to measure growth and the experimental settings differ between studies. Growth can be compared between different experimental conditions, standardized by plant size or age, measured once or over the entire plant ontogeny, and samples can be collected destructively or non-destructively (Pommerening & Muszta, 2016). These diverse approaches to measuring, calculating, and standardizing growth could contribute to the idiosyncratic and crop-specific responses of growth to domestication.

The differential effects of domestication on plant growth could also be explained by the heterogeneity of domestication processes (Purugganan & Fuller, 2009). Crops with diverse origins and histories may have evolved in response to different environmental pressures, human selection purposes, and over different time periods (Hufford *et al.*, 2019). For example, latitude and temperature at the geographic origin of each crop influence the response of leaf C, N, and P concentrations and ratios to domestication (Delgado-Baquerizo *et al.*, 2016). In addition, the effects of domestication on herbivore

resistance vary depending on human selection, such that crops selected for seed and fruit production show greater changes in herbivore resistance and damage compared to leaf crops (Whitehead *et al.*, 2016). Finally, some of the differences among crops in the effects of domestication on RGR could also be explained by phylogenetic relationships among species, as RGR and its components show phylogenetic signal (Kempel *et al.*, 2011; Atkinson *et al.*, 2016).

Our major crops were domesticated over the last c. 10,000 years, and modern varieties are the product of the last c. 100 years of intensive breeding for high-yielding crops. Here, we explore the extent to which domestication and modern plant breeding have impacted RGR and its components in a wide range of herbaceous crops. We conducted two experiments: an intensive one, in which the domestication history of durum wheat was addressed in detail, and an extensive one, in which 18 crop species were investigated more broadly. In both experiments, we grew multiple accessions of wild progenitors, landraces, and improved cultivars of each crop under common conditions and non-destructively measured their growth dynamics using a size-standardized approach (Rees *et al.*, 2010). By comparing landraces with their wild progenitors and with improved cultivars, we addressed the effects of domestication and modern breeding, respectively. To investigate differences among taxa, we also collected data on the origin and domestication history of each crop. Specifically, we asked: i) How have domestication (wild progenitors *vs.* landraces) and modern plant breeding (landraces *vs.* improved cultivars) impacted crop growth rates?; ii) Which components of RGR have changed the most during crop evolution?; and iii) Can changes in growth rates be explained by phylogeny, organ under selection, time in cultivation, and climate at crop origin?

MATERIAL AND METHODS

Two experiments were carried out to investigate how growth rates evolved after domestication and modern plant breeding. The first experiment, called the *intensive experiment*, examined in detail the variation in growth rate during the evolution of durum wheat (*Triticum turgidum* L.). The second experiment, the *extensive experiment*, explored growth rate changes after domestication and further improvement in a diverse set of 18 crops. In both experiments, we estimated total mass, leaf mass, and leaf area at different

times during the vegetative growth period on individual plants. Using non-linear growth models, we obtained the relative growth rate and its components at a common size. Finally, we computed the magnitudes and directions of domestication and improvement effects for all 19 crops and tested whether they varied as a function of the origin and history of domestication and phylogenetic relationships among species.

Study system

Over the course of crop domestication and subsequent improvement, three main domestication statuses can be distinguished: wild progenitors (W), the closest wild relatives contributing to the gene pool of the crop; landraces (L), domesticated genotypes that have not undergone intensive breeding in the last century and therefore most closely represent early domesticates; and improved cultivars (I), genotypes from more recent breeding programs (Abbo *et al.*, 2014). The identity of the putative wild progenitor of each crop was taken from the Crop Origins database (Milla, 2020; accessed 16 March 2021). Note that most crops are attributed a single wild progenitor, but some have several wild progenitor taxa, either due to knowledge gaps, taxonomic uncertainties, or hybrid origins. In addition, wild progenitors are thought to represent the closest extant wild taxa, rather than the original ancestral populations of the domesticated gene pool.

In both experiments, we grew several accessions belonging to the three domestication statuses and covering a wide range of geographical origins (Fig. 1a). For the *intensive experiment*, 32 accessions summarizing the domestication history of durum wheat were selected. In particular, eight accessions of wild emmer wheat (*T. turgidum* L. ssp. *dicoccoides* (Asch. & Graebn.) Thell.), eight accessions of early landraces (domesticated emmer originating c. 10,000 years ago; *T. turgidum* L. ssp. *dicoccum* (Schrank ex Schübl.) Thell.), eight accessions of late landraces (domesticated durum originating c. 7,000 years ago; *T. turgidum* L. ssp. *durum* (Desf.) Husn.), and eight accessions of modern wheat (*T. turgidum* L. ssp. *durum* (Desf.) Husn.) (Matsuoka, 2011; Roucou *et al.*, 2017). For the *extensive experiment*, we selected 18 phylogenetically diverse herbaceous species, mostly annuals, belonging to different functional groups (Table 1). About 26% of them were cereals, 26% legumes, and 48% forbs (*i.e.* herbaceous flowering plants that are neither graminoids nor legumes). These species have C_3 photosynthesis, except for *Amaranthus*, *Pennisetum*, and *Sorghum*, which have C_4 photosynthesis. For each species, we selected three wild accessions, two landrace

accessions, and two improved accessions, for a total of 126 accessions (see Supporting Information Table S2 and Table S3 for accessions identifiers and seed donors).

Experimental procedures

The *intensive* and *extensive experiments* were conducted in spring 2018 and 2019, respectively. In both experiments, 12–35 seeds per accession were randomly selected and individually sown on peat-filled flats. Those with thick and/or hard testas (mostly legumes) were first scarified with a wire cutter to facilitate seed imbibition. About two weeks after sowing, seedlings were transplanted into 3.6-l square pots (15 x 15 x 20 cm) containing washed sand and slow-release fertilizer (5 g l^{-1} Basacote Plus 6M; Compo, Barcelona, Spain). The amount of fertilizer was set according to the manufacturer's recommended dose for high nutrient availability conditions. Pot size was chosen to allow unrestricted growth for the largest species following the recommendations of Poorter *et al.* (2012). All pots were randomly placed on two contiguous benches in the CULTIVE glasshouse of the Universidad Rey Juan Carlos (Madrid, Spain) and received full sun (mean photosynthetically active radiation during light hours (10:00–20:00 h), PAR ± SD = 892 ± 204 μmol m^{-2} s^{-1}). Pots were watered regularly to ensure adequate water supply, and air temperature (T) and relative humidity (RH) in the glasshouse were recorded hourly (*intensive experiment*, mean T ± SD = 16.1 ± 8.1 °C, mean RH ± SD = 68 ± 22.6%; *extensive experiment*, mean T ± SD = 23.9 ± 5.2 °C, mean RH ± SD = 57.2 ± 15.5%).

Each experiment was divided into two groups: the focal and calibration plants. In the focal plants, we measured several traits (see below) non-destructively at regular intervals during the vegetative growth period. In the calibration plants, we measured the same traits but also harvested individuals at regular intervals to obtain the dry mass of leaves and the whole plant, and total leaf area. Calibration plants were used to develop statistical models predicting the dry mass of leaves and plants and total leaf area from the non-destructively measured traits. These models were then used to estimate the masses and areas of focal plants at each monitoring date. Below we describe the experimental procedures used, while the mathematical methods to estimate biomass from the non-destructive traits are described in the Mass Estimations subsection of Data Analyses.

For focal plants, six and three plants per accession were used in the *intensive* (N = 192 focal plants) and *extensive* (N = 378 focal plants) *experiments*, respectively. Each

plant was monitored individually every three to ten days (8–12 times in total); more frequently during early growth. During monitoring, the following non-destructive traits were measured: plant height, canopy diameter, number of branches, number of leaves, and length of the longest leaf. Basal stem diameter was also measured using a digital calliper (0.01 mm resolution), but only in the *extensive experiment*, as wheat showed little variation in this trait.

For calibration plants, six to nine destructive harvests were conducted during the vegetative growth period. At each harvest, one plant per accession (*intensive experiment*) or one plant per species and domestication status (either wild or domesticate; *extensive experiment*) was harvested after measuring the non-destructive traits. Harvested plants were washed and divided into stems, leaves, roots, leaf litter and reproductive fraction (buds, flowers and fruits). Petioles and rachises were included in the stem fraction. We scanned all leaf laminae at a 400-dpi resolution and measured the total leaf area per plant using Photoshop software (CS6; Adobe Systems, Inc., San Jose, CA, USA). Each plant fraction was dried at 60 °C for three days and weighed to the nearest mg. Total mass (g) per plant was computed as the sum of all mass fractions at each harvest date.

Data compilation on phylogeny, origin and history of crops

We built a phylogeny with our set of 19 crops (Fig. 1b). This phylogenetic tree was pruned from the most comprehensive tree to date for angiosperms (Qian & Jin, 2016) using the *drop.tip* function of the 'phytools' R package (Revell, 2012). *Abelmoschus esculentus* was not in the reference tree, so its placement was taken as that of a sister Malvaceae (*Hibiscus sabdariffa*), included in the reference tree. We also collected data on time in cultivation (*i.e.* earliest record of exploitation in cultivation (ya)) and organ under artificial selection (either fruits, leaves, or seeds) (Fig. 1c) from the Crop Origins database (Milla, 2020; accessed 16 March 2021). The geographic location (latitude and longitude) of each accession was also searched on the website of the corresponding germplasm bank (Fig. 1d, Supporting Information Table S2 and Table S3). For each location, past climatic data on temperature and precipitation regimes (Fig. 1e) were obtained as follows. Considering the large climatic variability during the Holocene, time in cultivation was divided into three periods according to available global paleoclimatic models: early-Holocene (11,700–8,300 years BP), mid-Holocene (8,300–4,200 years BP), and late-Holocene (4,200 years BP to present). Then, for crops originating in the late-, mid-, or

early-Holocene, we used their respective paleoclimatic model from the PaleoClim database at ~5 km resolution (www.paleoclim.org; Brown *et al.*, 2018). Models were read into R using the *raster* function of the 'raster' R package (Hijmans, 2021). Of the 19 bioclimatic variables provided, six were selected for the primary analyses, including mean annual temperature, total annual precipitation, temperature seasonality, precipitation seasonality, temperature of the coldest quarter, and precipitation of the driest quarter. This selection aimed to cover annual trends, seasonality, and extreme conditions. We calculated the arithmetic mean of the bioclimatic variables for each location and species as a proxy for the climate at the geographic origin of each crop.

Data analyses

Prior to data analysis, four dead individuals from the *intensive experiment* were excluded from the data set, as was one individual from the *extensive experiment* that was a clear outlier. All analyses were performed separately for each experiment in R v.4.1.1. (R Core Team, 2021).

Mass estimations

Linear regressions were performed to obtain prediction equations for total mass, leaf mass, and leaf area using data from the calibration plants. Trait, mass, and area variables were $\log_e$-transformed. We fitted linear mixed-effects models (LMM) to account for the factorial design of the experiments. Models were run with the response variable (*i.e.* total plant mass, leaf mass, or leaf area), the non-destructive trait measurements as fixed-effects predictors, and harvest date as a covariate. The random effects structure varied between experiments. In the *intensive experiment*, accession identity was included as a random effect over the intercept, whereas in the *extensive experiment*, a combined variable between crop identity and domestication status (either wild or domesticate) was used. To allow the relationship between the response variable and predictors to vary across accessions in the *intensive experiment* and between species and domestication status (combined variable) in the *extensive experiment*, we included a random slope effect over the non-destructive trait measurements.

For model selection, we looked for the optimal fixed structure by fitting models with all combinations of fixed-effects predictors. The inclusion/exclusion of random effects over the slopes depended on the presence/absence of certain predictors. Model

selection was based on the minimum AIC value. Selected models explained a great proportion of the variation in the response variable (*intensive experiment*, mean R^2m ± SD = 0.98 ± 0.004, mean R^2c ± SD = 0.99 ± 0.004; *extensive experiment*, mean R^2m ± SD = 0.86 ± 0.040, mean R2c ± SD = 0.99 ± 0.002) and were used to predict total mass, leaf mass, and leaf area of focal plants (see Supporting Information Methods S1 for more details). All models were run with the *lmer* function of the 'lme4' R package (Bates *et al.*, 2015) with maximum likelihood (ML) estimation.

Curve fitting

We fitted logistic functions to the increase in mass of focal plants over the vegetative growth period. Logistic functions are commonly used to describe biological growth patterns and are appropriate when the data span the entire vegetative lifespan (Paine *et al.*, 2012). Specifically, the three- and four-parameter logistic models were tested and implemented with the *SSlogis* and *SSfpl* functions, respectively, in the 'nlme' R package (Pinheiro *et al.*, 2021). We modelled $\log_e$(total mass) as a function of time, adding plant identity as a random factor to all curve parameters (*i.e.* curve parameters were allowed to vary among individuals). For both experiments, the most parsimonious model based on minimizing AIC was the four-parameter logistic model (Supporting Information Fig. S1) which modelled the variation of $\log_e$(total mass) ($\log_e M$) over time (t) as follows:

$$\log_e M = A + \frac{B-A}{1+ e^{(xmid-t)/scal}} \qquad \text{(Eqn 1)}$$

where *A*, *B*, *xmid*, and *scal* are the free parameters. Parameters *A* and *B* are the minimum and maximum asymptotic $\log_e$(mass), respectively; *xmid* is the time at which $\log_e$(mass) is midway between the minimum and maximum asymptotes, and *1*/*scal* is the slope at the inflection point (Richards, 1959; R function *SSfpl* in Pinheiro *et al.* (2020)). A separate curve was fitted for $\log_e$(leaf mass) and $\log_e$(leaf area) following the same steps, and again the four-parameter logistic function provided the best fit.

RGR Calculation

To compare relative growth rates between plants at a common size, we extracted the curve parameters from the fitted model and calculated a size-standardized relative growth rate (sRGR) as:

$$sRGR = \frac{(1/scal)(A-\log_e M_C)(B-\log_e M_C)}{(A-B)} \qquad \text{(Eqn 2)}$$

where $\log_e M_C$ is the common $\log_e$(mass) (Rees *et al.*, 2010). We used the median of the mass distribution across all focal plants as the common size because all species occurred

at this size (0.555 g in the *intensive experiment* and 0.383 g in the *extensive experiment*). Plant mass in the data set ranged from 0.006 g to 17.910 g in the *intensive experiment* and from 0.001 g to 66.836 g in the *extensive experiment.* Because our size-standardized metric focused on small plants, we supplemented it with metrics based on ontogenetic criteria. In particular, we calculated the time-standardized RGR (tRGR) at two ontogenetic stages: seedling and adult. Because the correlations among the three RGR metrics were very high (Supporting Information Fig. S2), we used the common size criteria for the analyses shown in the body of the paper to control for the widely reported effects of plant size on RGR (Evans, 1972; Grime & Hunt, 1975; Rees *et al.*, 2010).

Components of RGR

Size-standardized RGR components were calculated from sRGR following Rees *et al.* (2010). On logarithmic scales, sRGR can be expressed as the sum of its components:

$$\log_e(sRGR) = \log_e(sNAR) + \log_e(sLMR) + \log_e(sSLA) \qquad \text{(Eqn 3)}$$

These components are functions of total mass (*M*), leaf mass (*ML*), and leaf area (*AL*) as follows:

$$\log_e(sRGR) = \log_e\left(\frac{1}{AL_C}\,\frac{M_C - M_0}{t_C - t_0}\right) + \log_e\left(\frac{ML_C}{M_C}\right) + \log_e\left(\frac{AL_C}{ML_C}\right) \qquad \text{(Eqn 4)}$$

To calculate the contribution of each growth component to sRGR, we first calculated the time (t_C) at which each focal plant reached the common mass (M_C) using the four-parameter logistic equation (Eqn 1). This allowed us to calculate the corresponding values of leaf mass (ML_C) and leaf area (AL_C) reached at that time from their respective fitted curve. We used the estimates of ML_C and AL_C to calculate size-standardized LMR (sLMR) and SLA (sSLA) applying equation 4. The value of NAR at the common mass (sNAR) was then estimated as the ratio between sRGR and the product of sLMR and sSLA (Eqn 3). For a detailed description of the calculation of growth traits, see Supporting Information Methods S2.

Relative importance of RGR components

We decomposed the variation in sRGR into its three components, following the protocol described by Rees *et al.* (2010). Briefly, the variance of $\log_e(sRGR)$ was equated to the sum of the variances and covariances of the three $\log_e$-transformed sRGR components. The relative importance of each component to sRGR variation was then calculated as the

sum of the absolute values of the component's variance and covariances divided by the sum of the absolute values of all variances and covariances.

Domestication and breeding effect size calculations

Hedges' *G* statistic was computed to measure the magnitude and direction of domestication and improvement effects on sRGR and its components. For domestication, this was calculated as the difference in means between landraces and wild progenitors of each crop divided by the pooled and weighted standard deviation of the two groups (Hedges *et al.*, 1999). In the *intensive experiment*, early and late landraces were considered together to make the two experiments comparable. Effect sizes of modern breeding on sRGR and its components were computed in the same way, but using improved cultivars and landraces as reference groups. Hedges' *G* and its 95% confidence interval were calculated using the *cohen.d* function of the 'effsize' R package (Torchiano, 2020).

Statistical analyses

To assess the impact of domestication and improvement on sRGR, we ran linear mixed-effects models (LMMs) using the *lme* function in the 'nlme' R package (Pinheiro *et al.*, 2021). The models included sRGR as a response variable and domestication status (with functional group and their interaction in the *extensive experiment*) as fixed effects. Accession identity (nested within species in the *extensive experiment*) was included as a random factor over the intercept. Log_e-transformations were used to meet the assumptions of the models. In the presence of heteroscedasticity (checked with Levene's and Bartlett's test), the variance structure of the data was modelled, with the best variance structure determined by comparing AIC and standardized residual plots (Zuur *et al.*, 2009). Specifically, the variance structure of the data was modelled using the *weights* option (VarIdent command) within the *lme* function. The significance of the fixed factors of the models was estimated using the *anova.lme* function with marginal (type III) sums of squares in the 'nlme' R package (Pinheiro *et al.*, 2021). The amount of variance explained by the models was quantified by calculating the marginal and conditional pseudo-R^2 with the *r.squaredGLMM* function from the 'MuMIn' R package (Barton, 2020). Multiple comparison tests among all levels and interactions of the fixed-effect factors were applied with false discovery rate control, using the *glht* function in the 'multcomp' R package (Hothorn *et al.*, 2008).

We investigated whether the effect sizes of domestication and modern breeding on growth traits could be explained by phylogenetic relationships. We calculated the phylogenetic signal in the effect sizes (Hedges' *G*) on growth traits (*i.e*. sRGR, sNAR, sLMR, and sSLA) using Blomberg's *K* statistic (Blomberg *et al.*, 2003). *K* values near zero indicate a lack of phylogenetic dependence, and values near one mean that closely related species tend to have more similar values than species drawn randomly from the tree. The significance of *K* values was tested using randomization tests with 1,000 permutations. To calculate *K* statistics and their significance we used the *phylosig* function of the 'picante' R package (Kembel *et al.*, 2010).

We performed phylogenetic generalized least squares models (PGLSs) to assess whether the effect sizes of domestication and modern breeding on sRGR and its components were explained by the origin and history of crops. PGLSs incorporate phylogenetic correlation structure in model residuals to account for phylogenetic non-independence of species (Symonds & Blomberg, 2014). Domestication and improvement effects on sRGR and its components were included as response variables, while organ under artificial selection, time in cultivation and bioclimatic variables as predictors. Models were run separately for each response and predictor variable. Because C_3 and C_4 species differ in their climate optima, the models for climate effects included the two-way interaction with photosynthetic pathway (Yamori *et al.*, 2014). Prior to analyses, precipitation-related variables were log-transformed. PGLSs were implemented using the *gls* function of the 'nlme' R package (Pinheiro *et al.*, 2021). To account for heteroscedasticity, the variance structure of the data was modelled using the weights option (VarIdent command) within the *gls* function. The significance of fixed factors was estimated using the *anova* function with marginal (type III) sums of squares in the 'nlme' R package (Pinheiro *et al.*, 2021). In models for bioclimatic variables, significance levels were adjusted for false-discovery rates with the *p.adjust* function of the 'stats' R package (R Core Team, 2021).

RESULTS

Evolution of RGR under cultivation

sRGR varied considerably among crops, ranging from 0.10 for peanut to 0.27 g g^{-1} d^{-1} for amaranth (global mean ± SD = 0.17 ± 0.06). We found no consistent change in sRGR

after domestication and subsequent plant breeding in any of the experiments (Table 2 and Table 3). The directions and effect sizes of domestication and improvement varied among crops (Fig. 2). The magnitudes of domestication effects on sRGR were significantly greater than those of subsequent plant breeding ($F_{1,95} = 15.95$, $P < 0.001$; Fig. 2).

In the *extensive experiment*, sRGR did not consistently differ with domestication status, but it differed significantly among functional groups (Fig. 3, Table 2). C_4 cereals had the highest and legumes the lowest average growth rates (0.24 and 0.11 g g^{-1} d^{-1}, respectively). In the *intensive experiment*, sRGR increased in domesticated plants when the entire domestication process was considered (*i.e*. wilds *vs*. all landraces; $F_{1,22} = 7.08$, $P = 0.014$), but when the domestication process was split, we found no effect of early or late domestication on sRGR in durum wheat (Fig. 4, Table 3). In both experiments, neither domestication nor modern breeding had consistent effects on growth curve parameters ($P > 0.05$ for each of the four fitted parameters; Supporting Information Fig. S3 and Fig. S4).

Responses of RGR components to domestication and breeding

None of the components of sRGR evolved consistently across species after domestication and modern breeding, with the exception of sSLA, which increased in improved cultivars (Table 2). Moreover, the high proportion of variance explained by the random structure in the *intensive experiment* indicated high variability in responses to domestication and improvement among the 32 durum wheat accessions (Table 3).

C_4 cereals and forbs had the highest sNAR and sLMR, respectively (Fig. 3, Table 2). Moreover, the effect of domestication varied among functional groups for sRGR and sLMR (interaction domestication status × functional group, Table 2). In the *intensive experiment*, sNAR increased and sLMR decreased when the entire domestication process was considered (*i.e*. wilds *vs*. all landraces; sNAR: $F_{1,22} = 6.81$, $P = 0.016$, and sLMR: $F_{1,22} = 6.40$, $P = 0.019$; Fig. 4); however, when considered separately, we found no effect of early and late domestication on any of the growth traits of durum wheat (Fig. 4, Table 3).

sRGR was positively correlated with sNAR ($F_{1,394} = 118.6$, $P < 0.001$; Supporting Information Fig. S5) and sSLA ($F_{1,394} = 8.9$, $P < 0.001$; Supporting Information Fig. S5),

whereas there was no relationship with sLMR ($F_{1,394}$ = 1.6, P = 0.204). sNAR was by far the main driver of variation in sRGR in both experiments (relative importance of NAR ± SD = 0.52 ± 0.02), followed by sLMR and sSLA (relative importance of sLMR ± SD = 0.28 ± 0.15; and of sSLA ± SD = 0.20 ± 0.14; Supporting Information Fig. S6).

Factors influencing domestication and improvement effects

Differences among crops in the effect sizes of domestication and improvement on sRGR, sNAR, sLMR, and sSLA were partially explained by the organ under artificial selection (Table 4). In crops selected for fruits, sNAR tended to increase after domestication, whereas in those selected for leaves and seeds, sLMR and sSLA increased (Fig. 5a, Table 4a). Only the increase in sLMR in leaf crops continued after improvement, leading to an increase in sRGR (Table 4b).

The relationships between climate at crop origin and effect sizes of domestication on growth traits were modulated by the photosynthetic pathway. For mean annual temperature and temperature of the coldest quarter, C_3 species showed an increase in sRGR and sNAR, a decrease in sLMR, and no effect on sSLA, while C_4 species showed the inverse relationships (Fig. 5b, Table 4a). Temperature seasonality showed the opposite patterns for the same traits (Table 4a). Precipitation-related variables hardly explained the effect sizes of domestication on sRGR components (Table 4a, Supporting Information Table S4). Variation in effect sizes of modern breeding among crops was statistically explained by some bioclimatic variables, such as temperature seasonality, in the same direction as domestication effects on C_3 species (Table 4b, Supporting Information Table S5).

Time in cultivation did not significantly explain the variation in effect sizes of domestication and improvement on sRGR and its components (Table 4). Effect sizes on sSLA showed a significant phylogenetic signal, suggesting that changes in sSLA during domestication tended to be similar in magnitude and direction in phylogenetically related species (Table 4a). The size and magnitude of modern breeding effects did not show phylogenetic signals (Table 4b).

DISCUSSION

In this study, we examined the evolution of RGR and its components during domestication and modern plant breeding in a wide range of herbaceous crops. We found that crops responded differently to domestication, suggesting that high yields, typical of agricultural plants, were not consistently accompanied by an increase in growth rates. These differential responses of RGR and its components to domestication and further plant breeding were dependent on the phylogeny, organ under selection, and climate at the geographic origin of each crop. Moreover, domestication affected RGR components in opposite directions, resulting in no or smaller net effects on RGR. Thus, the evolution of RGR was also constrained by trade-offs between its underlying components.

Evolution of growth rates under cultivation

We found that size-standardized RGR changed from wild progenitors to landraces to improved cultivars in idiosyncratic ways, *i.e*. the direction and magnitude of the effects of domestication and modern breeding differed among crops. Of the 19 crops studied, six had a negative effect size, four had a positive effect size, and nine showed no effect (based on 95% CIs, Fig. 3). This species-specific response of RGR is consistent with previous studies that focused on individual crops. For example, RGR increased with domestication in tomato (Conesa *et al.*, 2017), decreased in rice (Cook & Evans, 1983) and barley (Chapin *et al.*, 1989), but showed no effect in wheat (Evans & Dunstone, 1970), maize (Duncan & Hesketh, 1968) and millet (Evans & Bush, 1985). These studies were conducted under dissimilar conditions and with different methodologies. However, even when comparisons are made between plants of the same size and under the same conditions, the effects of domestication and improvement on growth rates vary widely among crops (Preece *et al.*, 2015; Simpson *et al.*, 2017). Our extensive screening, together with previous case studies, therefore supports the scenario of an inconsistent pattern of growth rate evolution during domestication and modern plant breeding.

The idiosyncratic changes in growth rates across crops contrast with the widely reported decline in defence investment during domestication and subsequent plant breeding (Rosenthal & Dirzo, 1997; Gepts, 2004; Meyer *et al.*, 2012; Chen *et al.*, 2015; but see Simpson *et al.*, 2017; Whitehead *et al.*, 2017). Plant defence theory predicts a trade-off between growth and defence because secondary metabolism and physical plant

structures are physiologically costly (Coley *et al.*, 1985). Trade-offs between growth and defence have been particularly well studied in natural ecosystems (Endara & Coley, 2011; Lind *et al.*, 2013), but have not been consistently supported in crops (Kempel *et al.*, 2011; Turcotte *et al.*, 2014; Simpson *et al.*, 2017; Moreira *et al.*, 2018). In wheat, barley, and maize, for example, silicon-based defences decreased after domestication, but growth rates did not (Simpson *et al.*, 2017). We speculate that reduced defence traits in crops are the result of early and direct selection for palatable and fast-growing wild progenitors and early domesticates, rather than the result of later selection through trade-offs with growth. Our results therefore raise the question of whether wild progenitors have faster growth rates and lower defensive traits than other wild species that have not been selected for agricultural purposes.

In this study, sNAR was the main driver of variation in sRGR, which is consistent with previous work (Shipley, 2006; Cunniff *et al.*, 2014; Atkinson *et al.*, 2016; but see Lambers & Poorter, 1992 and Wilson *et al.*, 1999 for contrasting results). However, the magnitude of change in sNAR during crop evolution was less than in sSLA and sLMR. Previous literature suggests that selection for higher yields has not altered crop physiology as much as allocation patterns and morphology (Gifford & Evans, 1981; Gifford *et al.*, 1984; Richards, 2000; Driever *et al.*, 2014; Sinclair *et al.*, 2019). For example, traits such as high harvest index (*i.e.* the ratio of yield to aboveground mass), lower allocation to chaff and pods, lower root mass fraction, or larger leaves and stems are more often claimed to drive yield (Evans & Dunstone, 1970; Donald & Hamblin, 1976; Sinclair, 1998; Waines & Ehdaie, 2007). In addition, other traits typically associated with the domestication syndrome, such as large initial and final body size, earlier reproduction, and lower branching have also contributed to higher yields (Preece *et al.*, 2015; Holland *et al.*, 2019; Houshmandfar *et al.*, 2020). In our study, the strong physiological basis of sRGR supports the notion that physiology has not consistently changed over the course of evolution under cultivation and is therefore not a major driver of variation in crop yield.

It is noteworthy that the changes in growth traits were greater after domestication than in later plant breeding. In fact, the magnitude of domestication effects was *c.* 74% greater than that of further breeding. This is consistent with other studies. For example, wild progenitors and landraces of wheat and maize show higher phenotypic diversity than

modern cultivars for root or kernel traits (Flint-Garcia *et al.*, 2009; Roucou *et al.*, 2017). One explanation for these results is that the domestication process, when broadly defined, *i.e*. from the initial domestication of wild progenitors to their spreading and diversification into landraces, spanned longer periods of time, whereas modern breeding practises began about a century ago (Faris, 2014). Moreover, the current study compared landraces with wild progenitors from diverse geographical regions, where natural selection pressures might be different. On the other hand, modern cultivars are derived from a limited number of landraces and intensive artificial selection for specific traits, which in turn has reduced phenotypic and genetic diversity (Tanksley & McCouch, 1997; Meyer & Purugganan, 2013). Therefore, wild progenitors and/or landraces harbour a greater diversity in growth traits compared to modern cultivars, which could lead to stronger effect sizes in the domestication process.

Factors explaining variation in domestication effects

Interestingly, the effect sizes of domestication on sRGR components were partially explained by the organ under selection. Specifically, fruit crops showed the highest domestication effects on sNAR, whereas leaf and seed crops showed larger effects on sSLA and sLMR. We are unaware of any previous studies reporting differential growth responses to domestication depending on which organ was primarily selected. Investment in fleshy fruits can be physiologically more costly than in leaves and seeds because they are typically photosynthetic sinks that require substantial amounts of carbon, nutrients, and water (Coombe, 1976). As a result, yields of fruit crops are often more limited by source strength (*i.e*. photosynthesis) rather than sink capacity (Li *et al.*, 2015), in contrast to what occurs in seed crops such as wheat, maize and soybean (Borrás *et al.*, 2004). Other physiological traits such as photosynthetic rate, stomatal conductance, and water and nutrient use efficiency may have accompanied the increase in sNAR during domestication of fruit crops; however, more evidence is needed to test this hypothesis. Furthermore, these results are in line with the idea that if sRGR does not differ between crops and their progenitors, this could be because domestication had opposite effects on the underlying components of RGR.

When C_3 and C_4 species were looked at separately, we found significant growth differences between crops from different geographic origins. After domestication, sRGR and sNAR tended to decrease with temperature and increase with seasonality in wild C_3

progenitors, whereas the opposite trend was observed in C_4 species (Supporting Information Fig. S7). For C_3 species, variation in growth rates with temperature is congruent with adaptation to the length of the growing season (T-plant physiology hypothesis; Reich & Oleksyn, 2004). Thus, previous studies showed faster growth rates in populations from regions with shorter growing seasons (either at high altitudes or high latitudes), both in crop progenitors (Alexander, 2010) and wild species (Weber & Schmid, 1998; Ryser & Aeschlimann, 1999; Milla *et al.*, 2009; but see Li *et al.*, 1998). In contrast, for C_4 species, the positive relationship between sRGR and sNAR with temperature is likely a result of the adaptive advantage that C_4 photosynthesis provides in regions with higher photorespiration and potential evapotranspiration losses (Watcharamongkol *et al.*, 2018). In our study, despite the low number of C_4 crops, we found that climate adaptations of wild progenitors modulated the growth response to domestication. The effect of domestication (*i.e.* landraces *vs.* progenitors) tended to be positive when wild C_3 progenitors came from regions with higher temperatures or lower seasonality, whereas C_4 showed the opposite trend. Similarly, Delgado-Baquerizo *et al.* (2016) found significant relationships between temperature at crop origin and changes during domestication in other growth-related traits such as leaf N, C, and P concentrations. Therefore, we speculate that wild C_3 and C_4 progenitors from regions with low and high temperatures (or high and low seasonal variation), respectively, already grew fast enough to meet agricultural needs or had reached their physiological limits and thus experienced little or even negative changes in plant growth during domestication. Exploring the specific adaptations of wild progenitors to climate could have important implications for our understanding of current crop performance and for future breeding and conservation programmes.

Variation in domestication effect sizes among crops was phylogenetically constrained only for sSLA, suggesting that phylogeny can partially explain the diversity of growth responses. Despite the fact that most growth traits showed significant effects of functional group (*i.e.* a factor largely related to phylogeny), common selection pressures during domestication and improvement may have favoured convergence in the direction and magnitude of growth traits changes among species in distant clades (Pickersgill, 2018). Finally, time in cultivation did not explain the differences in effect sizes of domestication and modern plant breeding on sRGR and its components. This result was also found for root traits in a number of crops (Martín-Robles *et al.*, 2018). It

has been suggested that evolutionary rates are similar to those measured for wild species (Purugganan & Fuller, 2011), or that they vary over time, both accelerating and decelerating depending on the prevailing selective force (Abbo & Gopher, 2020). For example, the spreading to new environments and intense directional selection have far greater potential for rapid evolutionary change than mutation or unconscious selection (Zeder, 2017). Therefore, time in cultivation may not be as relevant as other factors in explaining evolutionary changes in crop growth.

In conclusion, our comprehensive survey suggests that growth rates have not responded consistently to domestication and modern plant breeding, in line with previous case studies. Crop-specific responses of growth to domestication and improvement depended on artificial selection purposes and climate at crop origin, and were constrained by correlations between traits rather than phylogenetic position. Thus, in fruit crops, artificial selection changed the physiological component of growth, whereas in leaf and seed crops it changed the components related to allocation and leaf morphology. The specific adaptations of wild progenitors to the climate at their origins further modulated the evolution of growth rates. Overall, our study sheds light on the factors underlying the diversity of crop responses to evolution under cultivation. Research in this area should further explore the causes and consequences of this diversity, given the importance of growth rates to crop performance.

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TABLES

Table 1 Common and botanical names of the crop species used in the two experiments, as well as their domestication status (W = wild progenitor; D = domesticate) and functional group affiliations. In the *extensive experiment*, domesticate status refers to accessions belonging to both landraces and improved cultivars.

Common name	Botanical name	Domestication status	Functional group
Intensive experiment			
Emmer wheat	*Triticum dicoccoides* (Asch. & Graebn.) Schweinf.	W	C_3 cereal
	Triticum dicoccum (Schrank ex Schübl.)	D (early landrace)	
Durum wheat	*Triticum durum* Desf.	D (late landrace)	C_3 cereal
	Triticum durum Desf.	D (improved)	
Extensive experiment			
Barley	*Hordeum spontaneum* K.Koch	W	C_3 cereal
	Hordeum vulgare L.	D	
Oat	*Avena sterilis* L.	W	C_3 cereal
	Avena sativa L.	D	
Pearl millet	*Pennisetum glaucum* (L.) R.Br.	W	C_4 cereal
	Pennisetum glaucum (L.) R.Br.	D	
Sorghum	*Sorghum arundinaceum* (Desv.) Stapf	W	C_4 cereal
	Sorghum bicolor (L.) Moench	D	
Amaranth	*Amaranthus hybridus* L.	W	Forb
	Amaranthus cruentus L.	D	
Lettuce	*Lactuca serriola* L.	W	Forb
	Lactuca sativa L.	D	
Borage	*Borago officinalis* L.	W	Forb
	Borago officinalis L.	D	
Cabbage	*Brassica oleracea* L.	W	Forb
	Brassica oleracea L.	D	
Flax	*Linum usitatissimum* L.	W	Forb
	Linum usitatissimum L.	D	
Okra	*Abelmoschus tuberculatus* Pal & Singh	W	Forb
	Abelmoschus esculentus (L.) Moench	D	
Sesame	*Sesamum indicum* L.	W	Forb

	Sesamum indicum L.	D	
Chili pepper	*Capsicum baccatum* L.	W	Forb
	Capsicum baccatum L.	D	
Tomato	*Solanum pimpinellifolium* L.	W	Forb
	Solanum lycopersicum L.	D	
Faba bean	*Vicia narbonensis* L.	W	Legume
	Vicia faba L.	D	
Lentil	*Lens culinaris* ssp. *orientalis* (Boiss.) Ponert	W	Legume
	Lens culinaris Medik.	D	
Peanut	*Arachis monticola* Krapov. & Rigoni	W	Legume
	Arachis hypogaea L.	D	
Vetch	*Lathyrus cicera* L.	W	Legume
	Lathyrus sativus L.	D	
White clover	*Trifolium repens* L.	W	Legume
	Trifolium repens L.	D	

Table 2 Effects of domestication and improvement on size-specific relative growth rate (sRGR), net assimilation rate (sNAR), leaf mass ratio (sLMR), and specific leaf area (sSLA) in the *extensive experiment*. All models included a two-way interaction ('×') between domestication status (either Dom –wild *vs*. landrace– or Imp –landrace *vs*. improved–) and functional group (FG). Species nested within accession were considered as random factors. The table shows the $F_{\text{d.f.}}$ score and significance of predictor variables. Significant values ($P < 0.05$) are highlighted in bold. The variance of the models explained by the fixed effects is indicated by the marginal pseudo-R^2 (R^2m), and the variance explained by both the fixed and random effects is indicated by the conditional pseudo-R^2 (R^2c).

	Domestication (Wild – Landrace)					**Improvement** (Landrace – Improved)				
	Dom	**FG**	**Dom × FG**	R^2**m**	R^2**c**	**Imp**	**FG**	**Imp × FG**	R^2**m**	R^2**c**
	$F_{1,68}$	$F_{3,14}$	$F_{3,68}$			$F_{1,50}$	$F_{3,14}$	$F_{3,50}$		
sRGR	1.15	**9.06**	**3.17**	0.59	0.91	0.18	**10.3**	1.50	0.61	0.87
sNAR	0.04	**11.4**	0.40	0.68	0.95	2.05	**11.7**	1.45	0.74	0.98
sLMR	0.02	**24.8**	**4.25**	0.77	0.96	0.62	**22.7**	0.80	0.80	0.99
sSLA	1.57	2.13	0.74	0.22	0.92	**5.45**	1.90	2.70	0.21	0.96

Table 3 Effects of early domestication (earlyDom), late domestication (lateDom), and improvement (Imp) on size-specific relative growth rate (sRGR), net assimilation rate (sNAR), leaf mass ratio (sLMR), and specific leaf area (sSLA) in the *intensive experiment*. Accession was considered as a random factor. The table shows the $F_{\text{d.f.}}$ score and significance of predictor variables. Significant values ($P < 0.05$) are highlighted in bold. The variance of the models explained by the fixed effects is indicated by the marginal pseudo-R^2 (R^2m), and the variance explained by both the fixed and random effects is indicated by the conditional pseudo-R^2 (R^2c).

	Early domestication (Wild – Early Landrace)			**Late domestication** (Early landrace – Late landrace)			**Improvement** (Late landrace – Improved)		
	earlyDom $F_{1,14}$	R^2**m**	R^2**c**	**lateDom** $F_{1,14}$	R^2**m**	R^2**c**	**Imp** $F_{1,14}$	R^2**m**	R^2**c**
sRGR	2.67	0.12	0.72	1.62	0.08	0.72	0.97	0.05	0.82
sNAR	2.15	0.09	0.56	2.11	0.08	0.52	0.61	0.03	0.64
sLMR	2.71	0.13	0.82	0.32	0.02	0.88	1.24	0.06	0.80
sSLA	2.42	0.11	0.77	0.04	0.001	0.47	0.49	0.02	0.40

Table 4 Phylogenetic signal and the effects of organ under selection (Organ), time in cultivation (Time) and some bioclimatic variables –mean annual temperature (MAT), temperature seasonality (TS), temperature of the coldest quarter (TCQ), total annual precipitation (TAP), precipitation seasonality (PS), and precipitation of the driest quarter (PDQ) at the geographic origin of each crop– on changes in size-specific relative growth rate (sRGR), net assimilation rate (sNAR), leaf mass ratio (sLMR), and specific leaf area (sSLA) during (a) domestication (Hedges' $G_{L\text{-}W}$) and (b) improvement (Hedges' $G_{I\text{-}L}$). The table shows the Blomberg´s *K* statistic for growth trait changes as well as the $F_{d.f.}$ score and significance of predictor variables. Significant values ($P < 0.05$) are highlighted in bold. Models for the bioclimatic variables included the two-way interaction ('×') with photosynthetic pathway (Photo; C_3 *vs*. C_4) and their *P*-values were corrected for multiple testing using false discovery rate. Results for the remaining bioclimatic variables can be found in Supporting Information Table S4 and Table S5.

	Phylogenetic signal	Phylogenetic generalized least squares models																	
		Model A	Model B	Model C			Model D			Model E			Model F			Model G			Model H		
Effect size	**Blomberg's *K***	**Organ**	**Time**	**MAT**	**Photo**	**MAT × Photo**	**TS**	**Photo**	**TS × Photo**	**TCQ**	**Photo**	**TCQ × Photo**	**TAP**	**Photo**	**TAP × Photo**	**PS**	**Photo**	**PS × Photo**	**PDQ**	**Photo**	**PDQ × Photo**
(a) $G_{L\text{-}W}$		$F_{1,16}$	$F_{1,17}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$
sRGR	0.14	0.52	0.77	1.42	8.76	**12.1**	0.04	0.29	**17.2**	0.15	2.06	**7.95**	0.25	0.04	0.03	1.30	**25.4**	**25.2**	0.20	1.42	**18.0**
sNAR	0.17	**4.90**	0.46	2.50	4.62	**6.92**	6.58	8.04	**9.98**	**8.92**	2.08	**14.0**	0.83	0.83	0.87	0.03	3.06	3.19	0.84	2.27	2.86
sLMR	0.09	**5.85**	2.89	3.40	5.76	**7.98**	3.70	5.21	**49.6**	8.46	3.79	**34.8**	2.93	0.79	0.80	1.17	2.54	2.47	1.90	1.85	2.82
sSLA	**0.30**	**19.1**	1.28	0.21	0.75	0.64	1.02	0.04	0.07	0.27	0.38	0.07	0.55	0.02	0.03	0.55	4.91	5.20	0.13	0.25	7.27
(b) $G_{I\text{-}L}$																					
sRGR	0.11	**7.81**	1.39	0.80	0.15	0.20	**10.2**	5.30	0.78	**8.10**	1.60	2.07	1.77	10.6	**13.3**	2.29	0.50	0.29	5.07	0.48	0.23
sNAR	0.06	0.91	2.13	0.67	0.44	2.17	**29.1**	2.10	1.12	3.52	0.14	1.22	1.09	0.00	0.00	3.86	7.52	11.7	**6.18**	0.78	1.10
sLMR	0.08	**3.23**	0.55	0.07	1.94	2.60	**9.89**	3.33	5.13	5.37	1.39	5.09	2.54	0.01	0.01	3.40	0.38	0.26	5.02	0.11	7.51
sSLA	0.04	0.15	0.85	0.00	1.66	2.09	**33.6**	2.15	0.02	**6.95**	0.87	0.13	0.83	0.10	0.08	1.86	2.27	2.21	5.28	0.92	2.70

FIGURES

Fig. 1 Description of the study system. (a) Evolution under cultivation of durum wheat (included in the *intensive experiment*) and lettuce (included in the *extensive experiment*), from wild progenitors to landraces (domestication process) and from landraces to improved cultivars (improvement process). (b) Phylogeny of the 19 crop species studied and histogram of time in cultivation (*i.e.* earliest record of exploitation in cultivation) indicating photosynthetic pathway (C_3 *vs.* C_4) and major organ under artificial selection (either fruit, leaf, or seed) for each crop. (c) Geographical distribution of wild and landrace accessions. The distribution of wild progenitors was used to infer the geographic origins of each crop. (d) Climate distribution at the origin of C_3 and C_4 accessions for mean annual temperature and total annual precipitation. Drawings are based on observations from this study and previous descriptions in the literature (see *e.g.* Roucou *et al.* (2017) for wheat).

Fig. 2 Changes in growth traits during (a) domestication and (b) improvement of the 19 crops studied. The dots are the effect sizes estimated by Hedges' *G*, and the bars are the 95% confidence intervals. Negative scores of Hedges' *G* indicate negative effects of domestication or improvement on size-specific relative growth rate (sRGR), net assimilation rate (sNAR), leaf mass ratio (sLMR), and specific leaf area (sSLA), and vice versa for positive scores. Colours indicate functional group affiliation: C_3 cereals (yellow), C_4 cereals (blue), forbs (pink), and legumes (red). The *intensive experiment* was included in the plot (Wheat*).

Fig. 3 Size-specific (a) relative growth rate (sRGR), (b) net assimilation rate (sNAR), (c) leaf mass ratio (sLMR), and (d) specific leaf area (sSLA) in the *extensive experiment* – 18 crop species – plotted separately by functional group: C_3 cereals, C_4 cereals, forbs, and legumes, and by domestication status: wild (W), landrace (L), and improved (I) accessions. Boxplots show the median and 25^{th} and 75^{th} percentiles of the data, with whiskers extending to 1.5 times the interquartile range. Different letters denote significant differences at $P < 0.05$ after Tukey's post hoc test and false discovery rate correction.

Fig. 4 Size-specific (a) relative growth rate (sRGR), (b) net assimilation rate (sNAR), (c) leaf mass ratio (sLMR), and (d) specific leaf area (sSLA) in the *intensive experiment* –

durum wheat – plotted separately by domestication status: wild (W), early landrace (EL), late landrace (LL), and improved (I) accessions. Boxplots show the median and 25th and 75th percentiles of the data, with whiskers extending to 1.5 times the interquartile range. Different letters denote significant differences at $P < 0.05$ after Tukey's post hoc test and false discovery rate correction.

Fig. 5 Effect sizes of domestication (Hedges' $G_{L\text{-}W}$) on the size-specific relative growth rate (sRGR), net assimilation rate (sNAR), leaf mass ratio (sLMR), and specific leaf area (sSLA) of 19 crop species plotted against (a) the organ under artificial selection and (b) the mean annual temperature (MAT) at the geographic origin of each crop. Boxplots show the median and 25th and 75th percentiles of the data, with whiskers extending to 1.5 times the interquartile range. Different letters indicate significant differences at $P < 0.05$, after Tukey's post hoc test and false discovery rate correction. Solid lines represent the fitted phylogenetic generalized least squares models. Symbols indicate the photosynthetic pathway: C_3 (circles) and C_4 (triangles).

Fig. 1

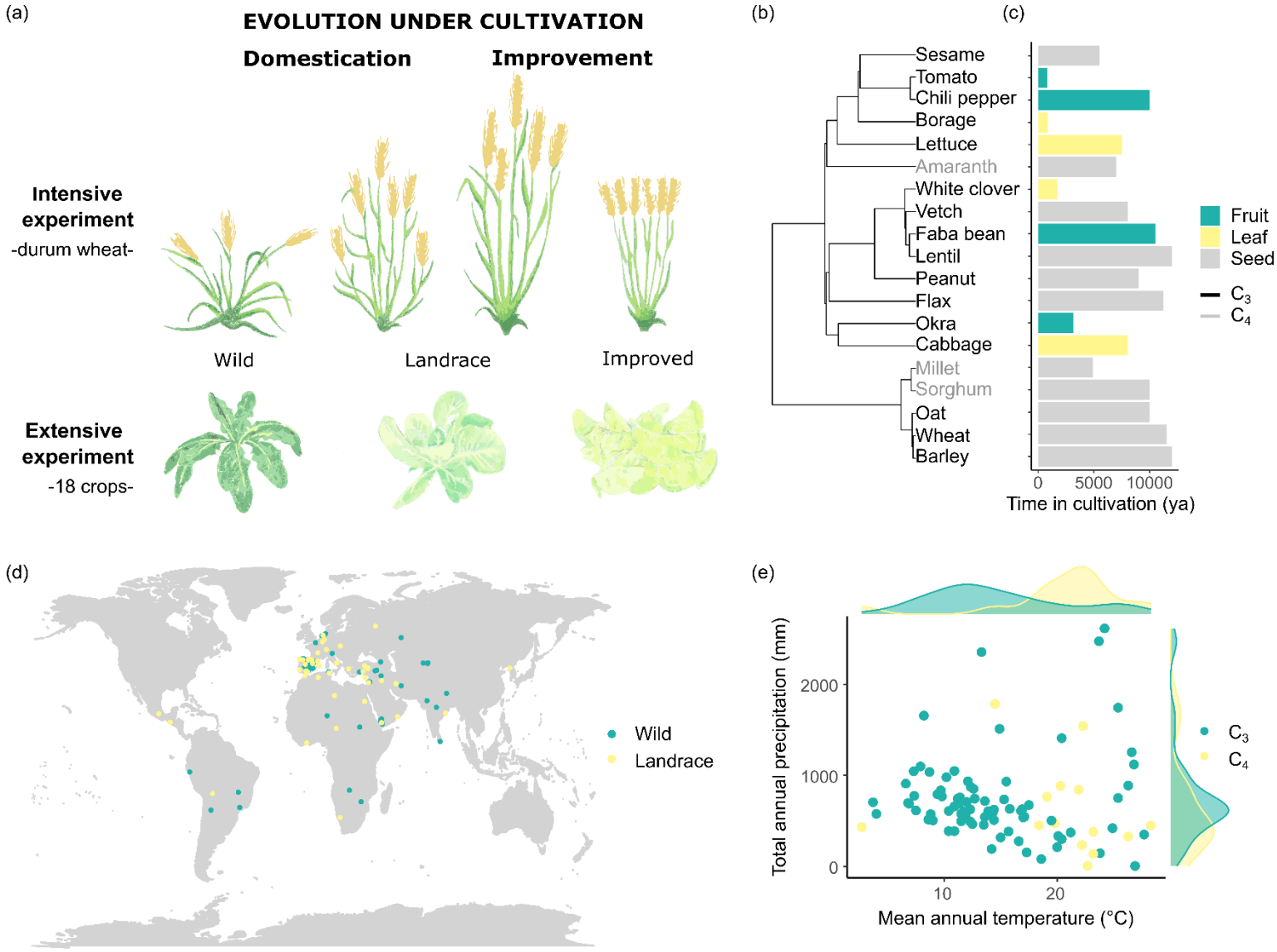

(a)
EVOLUTION UNDER CULTIVATION
Domestication
Improvement
Intensive experiment
-durum wheat-
Wild
Landrace
Improved
Extensive experiment
-18 crops-
(b)
(c)
Sesame
Tomato
Chili pepper
Borage
Lettuce
Amaranth
White clover
Vetch
Faba bean
Lentil
Peanut
Flax
Okra
Cabbage
Millet
Sorghum
Oat
Wheat
Barley
Fruit
Leaf
Seed
C3
C4
0
5000
10000
Time in cultivation (ya)
(d)
Wild
Landrace
(e)
Total annual precipitation (mm)
2000
1000
0
10
20
Mean annual temperature (°C)
C3
C4

Fig. 2

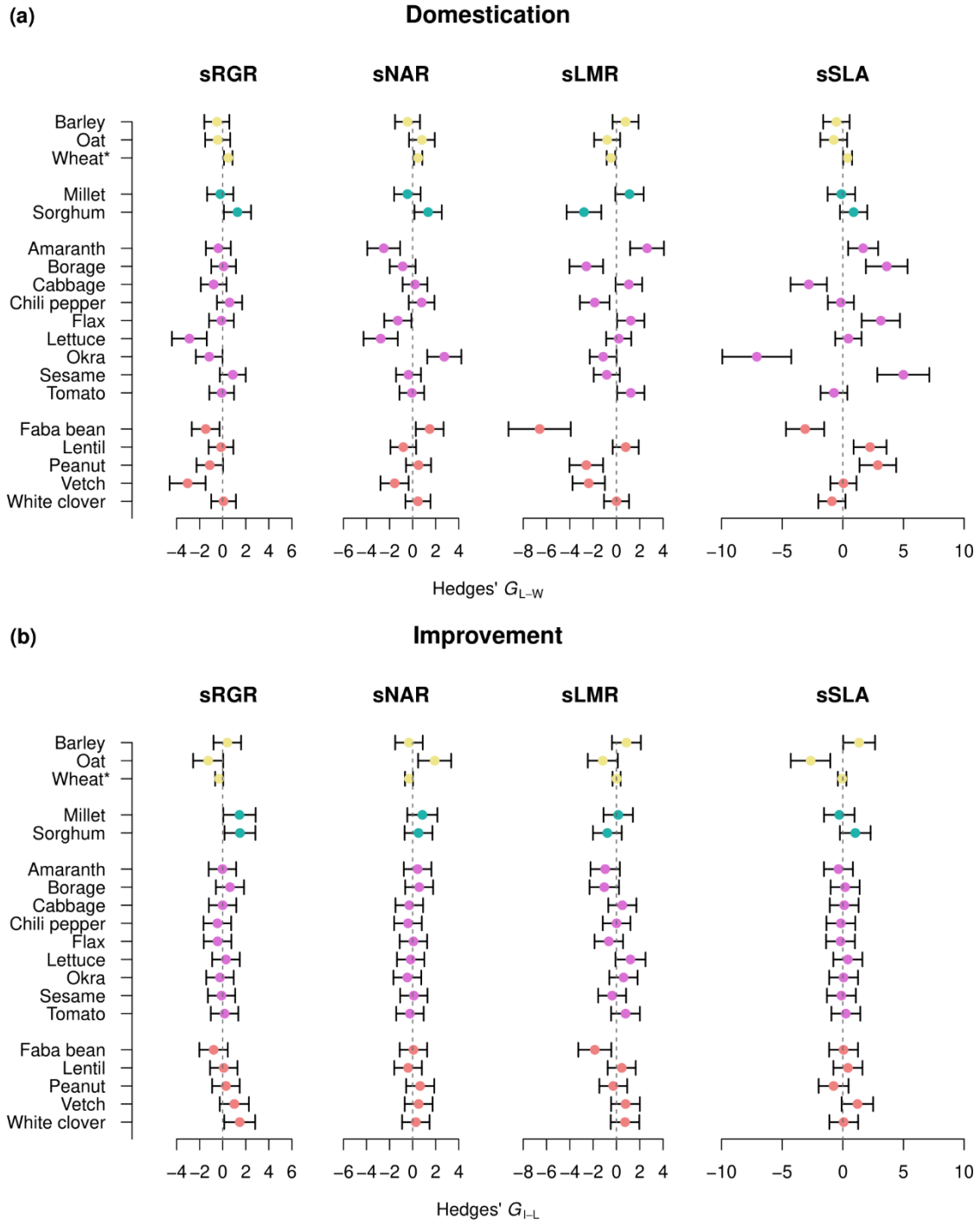

(a)
Domestication
sRGR
sNAR
sLMR
sSLA
Barley
Oat
Wheat*
Millet
Sorghum
Amaranth
Borage
Cabbage
Chili pepper
Flax
Lettuce
Okra
Sesame
Tomato
Faba bean
Lentil
Peanut
Vetch
White clover
−4 −2 0 2 4 6
−6 −4 −2 0 2 4
−8 −6 −4 −2 0 2 4
−10 −5 0 5 10
Hedges' G_{L-W}
(b)
Improvement
sRGR
sNAR
sLMR
sSLA
Barley
Oat
Wheat*
Millet
Sorghum
Amaranth
Borage
Cabbage
Chili pepper
Flax
Lettuce
Okra
Sesame
Tomato
Faba bean
Lentil
Peanut
Vetch
White clover
−4 −2 0 2 4 6
−6 −4 −2 0 2 4
−8 −6 −4 −2 0 2 4
−10 −5 0 5 10
Hedges' G_{I-L}

Fig. 3

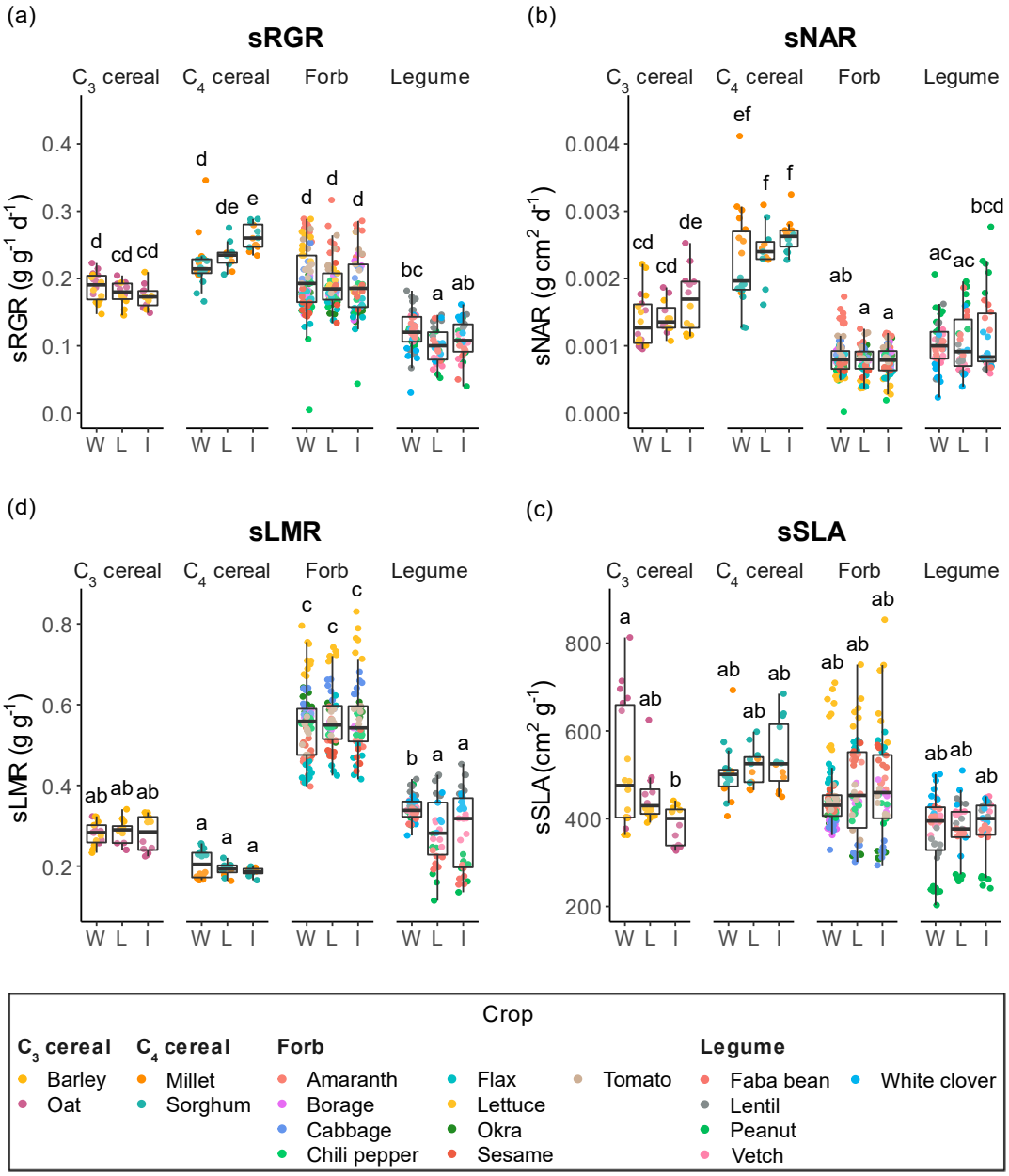
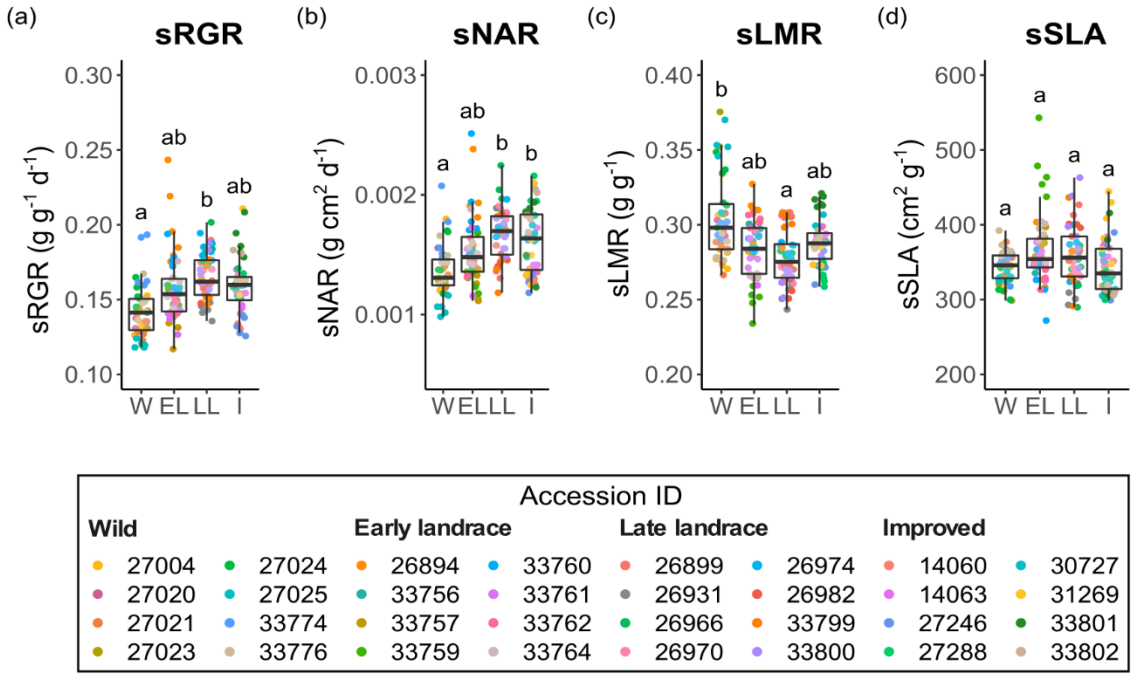

(a)
sRGR
sRGR (g g-1 d-1)
(b)
sNAR
sNAR (g cm2 d-1)
(d)
sLMR
sLMR (g g-1)
(c)
sSLA
sSLA (cm2 g-1)
C3 cereal
C4 cereal
Forb
Legume
W L I
Crop
C3 cereal
Barley
Oat
C4 cereal
Millet
Sorghum
Forb
Amaranth
Borage
Cabbage
Chili pepper
Flax
Lettuce
Okra
Sesame
Tomato
Legume
Faba bean
Lentil
Peanut
Vetch
White clover

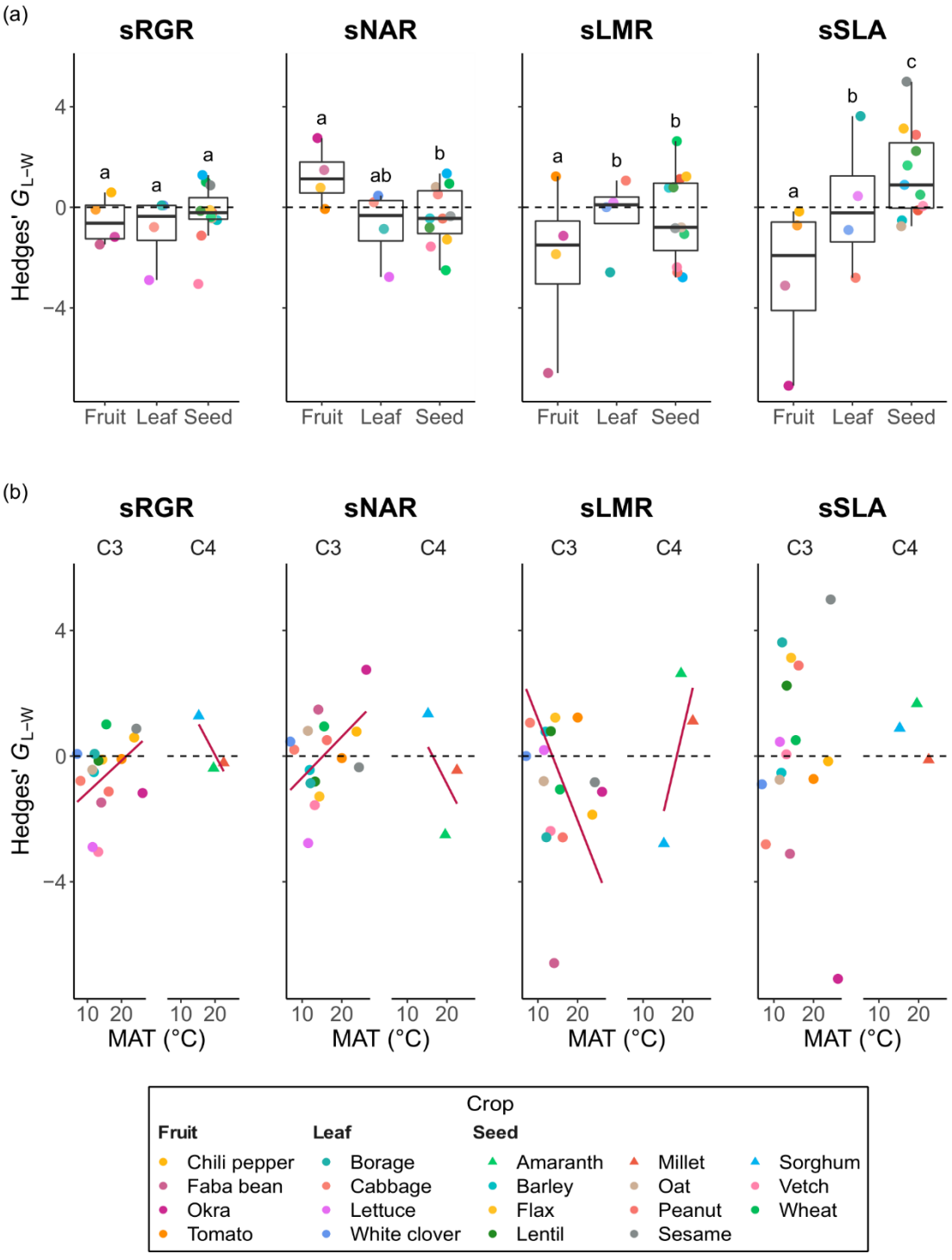
Fig. 4



Accession ID

Wild		Early landrace		Late landrace		Improved	
27004	27024	26894	33760	26899	26974	14060	30727
27020	27025	33756	33761	26931	26982	14063	31269
27021	33774	33757	33762	26966	33799	27246	33801
27023	33776	33759	33764	26970	33800	27288	33802

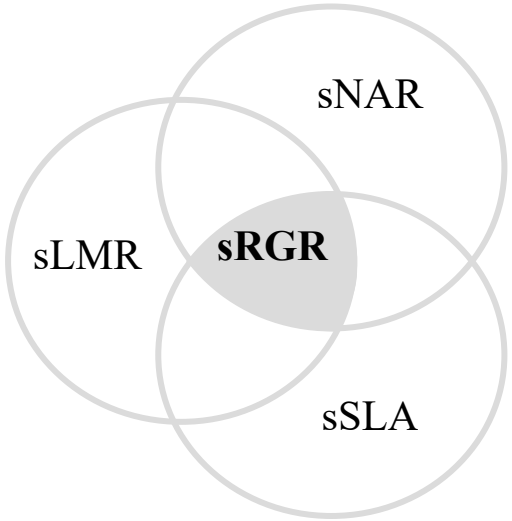
Fig. 5


(a)
sRGR
sNAR
sLMR
sSLA
Hedges' G_{L-W}
4
0
−4
a
a
a
a
ab
b
a
b
b
a
b
c
Fruit
Leaf
Seed
(b)
C3
C4
10
20
MAT (°C)
Crop
Fruit
Chili pepper
Faba bean
Okra
Tomato
Leaf
Borage
Cabbage
Lettuce
White clover
Seed
Amaranth
Barley
Flax
Lentil
Millet
Oat
Peanut
Sesame
Sorghum
Vetch
Wheat

SUPPORTING INFORMATION

Table S1 List of abbreviations, definitions, formulae, and units for the growth traits studied in the experiments, and a diagram showing the relationships among them.

Trait	Abbr.	Definition	Formula	Unit
Size-specific relative growth rate	sRGR	The rate of dry mass accumulation at a specific plant size per unit of existing dry mass	$\frac{1}{M}\frac{dM}{dt}$	g g^{-1} d^{-1}
Size-specific net assimilation rate	sNAR	The rate of total dry mass increase at a specific plant size per leaf area and time	$\frac{1}{AL}\frac{dM}{dt}$	g cm^2 d^{-1}
Size-specific leaf mass ratio	sLMR	The ratio of total dry mass allocation to the leaves at a specific plant size	$\frac{\mathrm{ML}}{\mathrm{M}}$	g g^{-1}
Size-specific specific leaf area	sSLA	The ratio of total leaf area to leaf dry mass at a specific plant size	$\frac{AL}{M}$	cm^2 g^{-1}



sRGR = sNAR x sLMR x sSLA

Table S2 Common and botanical names, family, functional group, domestication status, and seed origin information (country and geographic coordinates) for each accession used in the *extensive experiment*. Accession identifier refers to the code assigned by each seed donor, except for commercial companies (N.A. = not applicable). The country and coordinates (latitude and longitude) where seeds were originally collected are indicated (N.A. = not available). Seed donor (BGVCU: Banco de Germoplasma Vegetal de Cuenca, Spain; CGN: Center for Genetic Resources, The Netherlands; CITA: Centro de Investigación y Transferencia Agroalimentaria de Aragón, Spain; COMAV: Instituto Universitario de Conservación y Mejora de la Agrodiversidad Valenciana, Spain; CRF: Centro Nacional de Recursos Fitogenéticos-INIA, Spain; ICARDA: International Center for Agricultural Research in Dry Areas, Lebanon; IPK: Germplasm Bank of the Leibniz Institute of Plant Genetics and Crop Plant Research, Germany; NPGS: National Plant Germplasm System-USDA, U.S.A.; *: commercial company).

Common name	Functional group	Family	Botanical name	Domestication status	Accession identifier	Accession country	Latitude	Longitude	Seed donor
Barley	C_3 cereal	Poaceae	*Hordeum spontaneum* K.Koch	Wild	BGE025385	Morocco	N.A.	N.A.	CRF
					PI 662181	Turkey	37.746	39.661	NPGS
					BGE025389	Morocco	N.A.	N.A.	CRF
			Hordeum vulgare L.	Landrace	BGE011162	Morocco	35.574	-5.375	CRF
					BGE024314	Greece	38.537	22.622	CRF
				Improved	N.A.	N.A.	N.A.	N.A.	Battle*
					BGE000214	Spain	N.A.	N.A.	CRF
Oat	C_3 cereal	Poaceae	*Avena sterilis* L.	Wild	BGE049076	Spain	38.786	-0.263	CRF
					BGE049079	Spain	42.841	-1.676	CRF
					IG 100379 IFMI 3096	Turkey	N.A.	N.A.	ICARDA
			Avena sativa L.	Landrace	BGE008136	Spain	41.983	2.825	CRF
					BGE008166	Spain	42.483	-3.199	CRF
				Improved	N.A.	N.A.	N.A.	N.A.	Battle*
					BGE024681	Spain	N.A.	N.A.	CRF
Millet	C_4 cereal	Poaceae	*Cenchrus americanus* (L.) Morrone	Wild	PI 537068	Niger	17.767	8.950	NPGS
					PEN 1028	Yemen	14.083	44.167	IPK
					PEN 1048	Yemen	16.07	43.300	IPK

				Landrace	PEN 837	Tunisia	36.803	10.172	IPK
					PEN 687	Libya	26.633	13.633	IPK
				Improved	PI 586660	Burkina Faso	N.A.	N.A.	NPGS
					PEN 1257	Soviet Union	N.A.	N.A.	IPK
Sorghum	C_4 cereal	Poaceae	*Sorghum arundinaceum* (Desv.) Stapf	Wild	PI 524718	Sudan	12.723	29.804	NPGS
					PI 482605	Zimbabwe	-20.383	30.667	NPGS
					PI 539066	Soviet Union	52.453	56.224	NPGS
			Sorghum bicolor (L.) Moench	Landrace	PI 532206	Oman	17.333	54.000	NPGS
					PI 535999	Cameroon	12.117	14.750	NPGS
				Improved	PI 563327	Sudan	N.A.	N.A.	NPGS
					PI 563437	Chad	N.A.	N.A.	NPGS
Amaranthus	Forb	Amaranthaceae	*Amaranthus hybridus* L.	Wild	Ames 2072	Nepal	27.701	85.300	NPGS
					PI 500234	Zambia	-15.300	23.150	NPGS
					PI 652417	Brazil	-16.217	-47.917	NPGS
			Amaranthus cruentus L.	Landrace	Ames 2001	Ghana	N.A.	N.A.	NPGS
					PI 643050	Mexico	18.717	-98.750	NPGS
				Improved	AMA 169	Nepal	N.A.	N.A.	IPK
					Ames 15197	Argentina	N.A.	N.A.	NPGS
Lettuce	Forb	Asteraceae	*Lactuca serriola* L.	Wild	BGV009232	Spain	43.094	-6.253	COMAV
					BGE034705	Spain	40.517	-3.283	CRF
					LAC 1079	Italy	45.427	12.178	IPK
			Lactuca sativa L.	Landrace	BGV003526	Spain	42.601	-6.724	COMAV
					BGV001094	Spain	37.692	-4.480	COMAV
				Improved	N.A.	N.A.	N.A.	N.A.	Battle*
					BGV005752	Spain	N.A.	N.A.	COMAV
Borago	Forb	Boraginaceae	*Borago officinalis* L.	Wild	BGHZ5329	Spain	40.978	-0.055	CITA
					BGHZ2103	Spain	42.173	-0.029	CITA
					BGHZ4294	Spain	42.279	-5.100	CITA
				Landrace	BGHZ0363	Spain	40.976	-0.443	CITA
					BGHZ2340	Spain	42.388	-0.717	CITA
				Improved	N.A.	N.A.	N.A.	N.A.	Battle*

					N.A.	N.A.	N.A.	N.A.	Rocalba*
Cabbage	Forb	Brassicaceae	*Brassica oleracea* L.	Wild	CGN06903	France	50.180	1.483	CGN
					CGN18947	Germany	54.200	7.867	CGN
					CGN25455	Netherlands	53.310	5.622	CGN
				Landrace	CGN14079	Belgium	40.976	-0.443	CGN
					CGN15773	Portugal	42.388	-0.717	CGN
				Improved	N.A.	N.A.	N.A.	N.A.	Rocalba*
					N.A.	N.A.	N.A.	N.A.	Battle*
Flax	Forb	Linaceae	*Linum usitatissimum* L.	Wild	Ames 29165	Georgia	41.660	43.053	NPGS
					PI 231945	Belgium	N.A.	N.A.	NPGS
					PI 253972	Irak	35.479	43.419	NPGS
				Landrace	LIN 2020	Yemen	14.633	43.633	IPK
					LIN 2288	Colombia	N.A.	N.A.	IPK
				Improved	BGE030455	Spain	N.A.	N.A.	CRF
					PI 598151	Nepal	N.A.	N.A.	NPGS
Okra	Forb	Malvaceae	*Abelmoschus tuberculatus* Pal & Singh	Wild	Grif 12671	India	24.483	72.783	NPGS
					PI 639676	Sri Lanka	6.275	81.157	NPGS
					PI 639681	India	21.537	78.803	NPGS
			Abelmoschus esculentus (L.) Moench	Landrace	PI 489782	Ivory Coast	5.667	-4.167	NPGS
					PI 505564	Zambia	-27.417	17.167	NPGS
				Improved	N.A.	N.A.	N.A.	N.A.	Battle*
					PI 548700	India	N.A.	N.A.	NPGS
Sesamum	Forb	Pedaliaceae	*Sesamum indicum* L.	Wild	SESA 17	Yemen	15.333	43.000	IPK
					SESA 20	Yemen	15.210	43.340	IPK
					SESA 22	Yemen	16.339	43.704	IPK
				Landrace	SESA 4	North Korea	38.949	125.765	IPK
					SESA 5	Irak	33.354	43.779	IPK
				Improved	N.A.	N.A.	N.A.	N.A.	Rocalba*
					SESA 14	N.A.	N.A.	N.A.	IPK
Chili pepper	Forb	Solanaceae	*Capsicum baccatum* L.	Wild	CGN21515	N.A.	N.A.	N.A.	CGN
					CGN16973	Bolivia	-16.800	64.400	CGN

					CGN17025	Bolivia	-16.800	64.400	CGN
				Landrace	CGN16972	India	19.000	85.000	CGN
					CGN23260	Bolivia	-16.800	-64.400	CGN
				Improved	CGN21470	Chile	N.A.	N.A.	CGN
					CGN22181	Peru	N.A.	N.A.	CGN
Tomato	Forb	Solanaceae	*Solanum pimpinellifolium* L.	Wild	BGV007948	Peru	-7.200	-79.050	COMAV
					LYC 1	N.A.	N.A.	N.A.	IPK
					LYC 2671	N.A.	N.A.	N.A.	IPK
			Solanum lycopersicum L.	Landrace	LYC 15	Switzerland	47.148	8.526	IPK
					LYC 1014	Guatemala	14.835	-91.518	IPK
				Improved	N.A.	N.A.	N.A.	N.A.	Battle*
					N.A.	N.A.	N.A.	N.A.	Clause*
Faba bean	Legume	Fabaceae	*Vicia narbonensis* L.	Wild	IG 111590 IFVI 5266	Tunisia	37.284	9.836	ICARDA
					BGE031092	Spain	40.817	-3.617	CRF
					BGE031093	Spain	38.100	-3.083	CRF
			Vicia faba L.	Landrace	BGE022388	Spain	42.850	-1.767	CRF
					BGE031076	Spain	40.573	-5.060	CRF
				Improved	N.A.	N.A.	N.A.	N.A.	Rocalba*
					N.A.	N.A.	N.A.	N.A.	Battle*
Lens	Legume	Fabaceae	*Lens culinaris* ssp. *orientalis* (Boiss.) Ponert	Wild	PI 572374	Iran	31.067	56.350	NPGS
					PI 572399	Turkey	37.167	29.579	NPGS
					BCU001423	Turkey	N.A.	N.A.	BGVCU
			Lens culinaris Medik.	Landrace	PI 297287	Argentina	N.A.	N.A.	NPGS
					PI 298022	Turkey	39.996	32.867	NPGS
				Improved	N.A.	N.A.	N.A.	N.A.	Battle*
					PI 379368	Serbia	N.A.	N.A.	NPGS
Peanut	Legume	Fabaceae	*Arachis monticola* Krapov. & Rigoni	Wild	PI 263393	Brazil	-22.870	-47.077	NPGS
					PI 468196	Argentina	-24.117	-65.383	NPGS
					PI 497261	Argentina	-24.133	-65.383	NPGS
			Arachis hypogaea L.	Landrace	PI 602352	Brazil	N.A.	N.A.	NPGS
					Grif 373	Sudan	N.A.	N.A.	NPGS

				Improved	PI 538758	Burkina Faso	N.A.	N.A.	NPGS
					PI 550688	China	N.A.	N.A.	NPGS
Vetch	Legume	Fabaceae	*Lathyrus cicera* L.	Wild	BGE019570	Spain	40.200	-2.267	CRF
					BGE016953	Spain	39.917	-5.167	CRF
					BGE016954	Spain	39.550	-5.400	CRF
			Lathyrus sativus L.	Landrace	BGE014724	Spain	40.003	3.839	CRF
					BGE046719	Spain	42.803	-8.898	CRF
				Improved	LAT 440	India	N.A.	N.A.	IPK
					LAT 466	Soviet Union	N.A.	N.A.	IPK
White clover	Legume	Fabaceae	*Trifolium repens* L.	Wild	CGN22512	Uzbekistan	41.150	70.417	CGN
					CGN22513	Kyrgyzstan	40.980	73.183	CGN
					CGN22516	Kyrgyzstan	41.230	73.367	CGN
				Landrace	CGN21763	France	45.700	2.900	CGN
					CGN22506	Netherlands	53.500	6.267	CGN
				Improved	N.A.	N.A.	N.A.	N.A.	Intersemillas*
					CGN23145	Denmark	N.A.	N.A.	CGN

Table S3 Botanical name, domestication status and seed origin information (country and geographic coordinates) for each accession used in the *intensive experiment*. Accession identifier refers to the code assigned by each seed donor, except for commercial companies. The country and coordinates (latitude and longitude) where seeds were originally collected are indicated (N.A. = not available). All seeds come from INRA - CRB: Small grain cereals Biological Resources Centre, France. Durum wheat belongs to the functional group of C_3 cereals.

Botanical name	Domestication status	Accession identifier	Accession country	Latitude (°)	Longitude (°)
Triticum dicoccoides (Asch. & Graebn.) Schweinf.	Wild	27004	Israel	N.A.	N.A.
		27020	Israel	N.A.	N.A.
		27021	Israel	N.A.	N.A.
		27023	Syria	32.783	36.200
		27024	Iraq	N.A.	N.A.
		27025	Iraq	N.A.	N.A.
		33774	Turkey	37.920	40.55
		33776	Israel	32.867	35.533
Triticum dicoccum (Schrank) Schübl	Early landrace	26894	Algeria	34.800	3.117
		33756	Turkey	39.000	35.000
		33757	Iraq	32.000	53.000
		33759	Iran	32.000	53.000
		33760	Italy	41.283	15.100
		33761	Russia	57.600	39.867
		33762	Slovakia	48.731	17.406
		33764	Germany	51.500	7.000
Triticum durum Desf.	Late landrace	26899	Algeria	N.A.	N.A.
		26931	Pakistan	N.A.	N.A.
		26966	Egypt	24.091	32.899
		26970	Palestine	32.500	35.500
		26974	Russia	34.717	33.083
		26982	Spain	37.167	-3.600

		33799	Turkey	37.420	31.850
		33800	Turkey	38.750	34.850
Triticum durum Desf.	Improved	14060	France	N.A.	N.A.
		14063	France	N.A.	N.A.
		27246	France	N.A.	N.A.
		27288	France	N.A.	N.A.
		30727	France	N.A.	N.A.
		31269	France	N.A.	N.A.
		33801	France	N.A.	N.A.
		33802	France	N.A.	N.A.

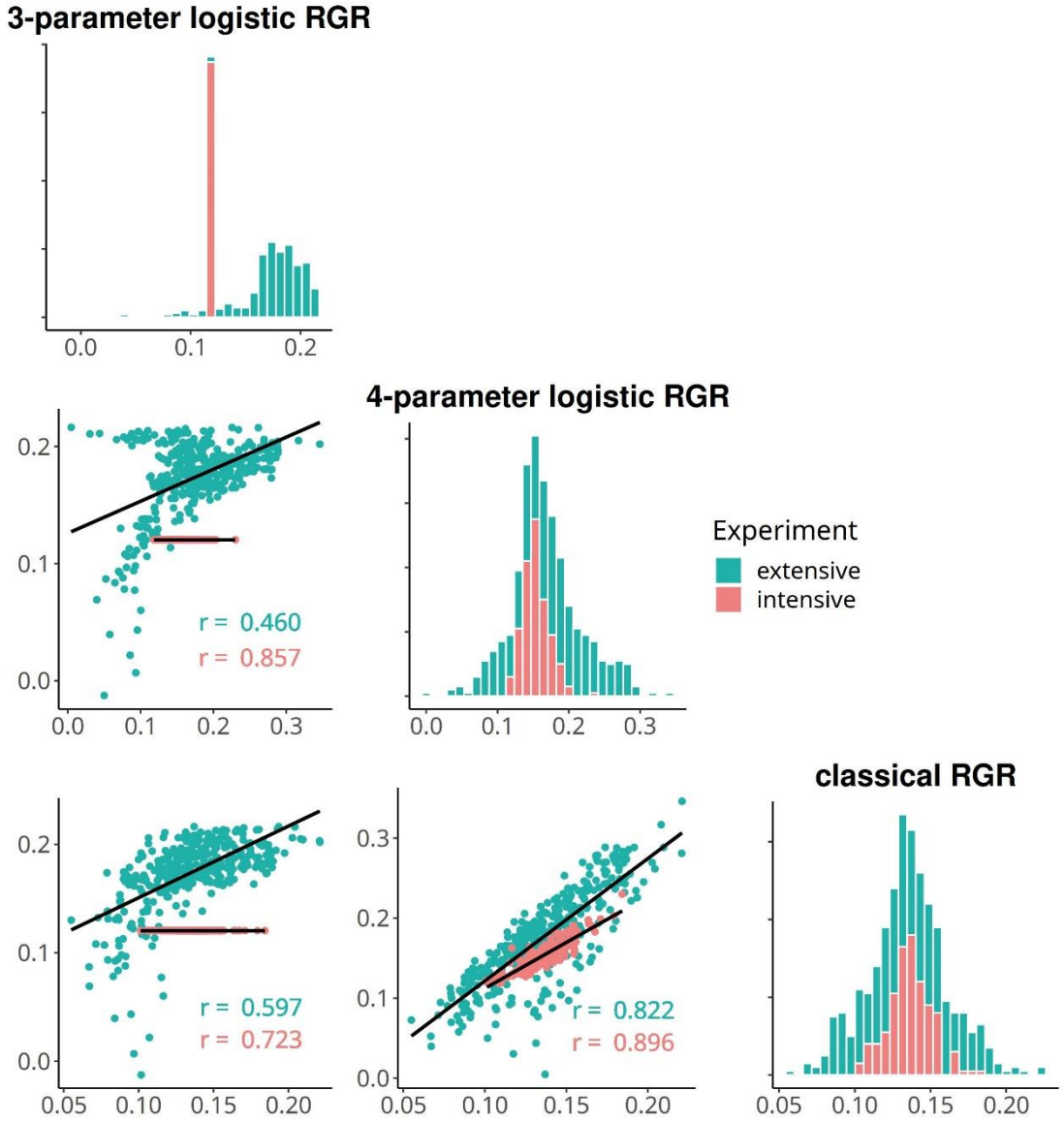
Table S4 Effects of the 19 bioclimatic variables at the geographic origin of each crop on the effect size of domestication (Hedges' $G_{L\text{-}W}$) on size-specific relative growth rate (sRGR), net assimilation rate (sNAR), leaf mass ratio (sLMR), and specific leaf area (sSLA). Models included the two-way interaction ('×') with photosynthetic pathway (Photo; C_3 *vs*. C_4). The table shows the $F_{d.f.}$ score and the significances of the predictor variables. Significant *P*-values ($P < 0.05$) are highlighted in bold after false discovery rate correction. Models were tested with phylogenetic generalized least squares. Abbreviations: BIO1, annual mean temperature; BIO2, mean diurnal range; BIO3, isothermality; BIO4, temperature seasonality; BIO5, maximum temperature of warmest month; BIO6, minimum temperature of coldest month; BIO7, temperature annual range; BIO8, mean temperature of wettest quarter; BIO9, mean temperature of driest quarter; BIO10, mean temperature of warmest quarter; BIO11, mean temperature of coldest quarter; BIO12, annual precipitation; BIO13, precipitation of wettest month; BIO14, precipitation of driest month; BIO15, precipitation seasonality; BIO16, precipitation of wettest quarter; BIO17, precipitation of driest quarter; BIO18, precipitation of warmest quarter; BIO19, precipitation of coldest quarter.

Response Hedges' $G_{L\text{-}W}$	**Predictors**	**1** $F_{1,15}$	**2** $F_{1,15}$	**3** $F_{1,15}$	**4** $F_{1,15}$	**5** $F_{1,15}$	**6** $F_{1,15}$	**7** $F_{1,15}$	**8** $F_{1,15}$	**9** $F_{1,15}$	**10** $F_{1,15}$	**11** $F_{1,15}$	**12** $F_{1,15}$	**13** $F_{1,15}$	**14** $F_{1,15}$	**15** $F_{1,15}$	**16** $F_{1,15}$	**17** $F_{1,15}$	**18** $F_{1,15}$	**19** $F_{1,15}$
sRGR	BIO	1.40	1.36	0.00	0.03	0.23	0.00	0.07	0.21	0.42	0.60	0.14	0.29	0.01	0.10	1.51	0.00	0.21	2.86	0.18
	Photo	8.78	1.84	**26.6**	0.30	1.73	0.74	1.20	5.26	3.26	3.26	2.07	0.04	1.26	0.93	**24.8**	0.92	1.44	2.09	0.56
	BIO × Photo	**12.1**	2.07	**55.4**	**17.6**	1.66	**6.60**	**20.8**	**5.54**	**10.3**	3.12	**7.96**	0.03	1.16	**17.6**	**24.4**	0.86	**18.1**	1.73	**18.5**
sNAR	BIO	2.50	5.52	0.01	6.97	1.91	8.85	7.66	10.13	0.47	0.79	8.76	0.75	2.32	0.29	0.04	1.73	0.79	0.25	0.89
	Photo	4.62	**56.1**	3.60	8.36	1.11	0.01	9.78	6.25	0.28	2.59	2.05	0.80	4.51	2.17	2.95	3.33	2.27	3.53	1.78
	BIO × Photo	**6.92**	**83.0**	3.93	**10.3**	1.17	**13.6**	**10.5**	**15.7**	1.75	2.76	**13.8**	0.84	4.80	2.94	3.08	3.49	2.87	3.86	2.86
sLMR	BIO	3.41	6.10	0.40	3.79	0.38	11.66	4.70	7.43	0.06	0.03	8.42	2.79	3.26	0.56	1.56	3.51	1.84	0.46	1.92
	Photo	5.77	**67.7**	3.43	5.37	1.38	0.11	**11.6**	**12.8**	1.15	3.03	3.75	0.74	4.36	1.73	2.32	3.37	1.85	3.18	1.34
	BIO × Photo	**7.99**	**127.1**	3.47	**49.9**	1.40	**16.3**	**61.6**	**24.8**	**6.32**	3.13	**34.7**	0.75	4.54	2.87	2.24	3.46	2.82	3.40	2.81
sSLA	BIO	0.21	4.68	0.25	0.95	0.99	0.55	1.27	1.00	0.68	1.07	0.32	0.61	0.70	0.00	0.45	0.35	0.14	1.15	0.15
	Photo	0.74	0.04	2.25	0.04	8.87	0.33	0.00	0.14	1.10	10.19	0.21	0.02	0.03	0.13	4.38	0.03	0.26	0.21	0.12
	BIO × Photo	0.63	0.06	2.88	0.07	9.70	0.03	0.07	0.05	2.87	**18.24**	0.12	0.03	0.02	4.52	4.55	0.02	7.39	0.13	7.14

Table S5 Effects the 19 bioclimatic variables at the geographic origin of each crop on the effect size of improvement (Hedges' $G_{I\text{-}L}$) on size-specific relative growth rate (sRGR), net assimilation rate (sNAR), leaf mass ratio (sLMR) and specific leaf area (sSLA). Models included the two-way interaction ('×') with photosynthetic pathway (Photo; C_3 *vs*. C_4). The table shows the $F_{d.f.}$ score and the significances of the predictor variables. Significant *P*-values ($P < 0.05$) are highlighted in bold after false discovery rate correction. Models were tested with phylogenetic generalized least squares. Abbreviations: BIO1, annual mean temperature; BIO2, mean diurnal range; BIO3, isothermality; BIO4, temperature seasonality; BIO5, maximum temperature of warmest month; BIO6, minimum temperature of coldest month; BIO7, temperature annual range; BIO8, mean temperature of wettest quarter; BIO9, mean temperature of driest quarter; BIO10, mean temperature of warmest quarter; BIO11, mean temperature of coldest quarter; BIO12, annual precipitation; BIO13, precipitation of wettest month; BIO14, precipitation of driest month; BIO15, precipitation seasonality; BIO16, precipitation of wettest quarter; BIO17, precipitation of driest quarter; BIO18, precipitation of warmest quarter; BIO19, precipitation of coldest quarter.

Response Hedges' $G_{I\text{-}L}$	**Predictors**	**1** $F_{1,15}$	**2** $F_{1,15}$	**3** $F_{1,15}$	**4** $F_{1,15}$	**5** $F_{1,15}$	**6** $F_{1,15}$	**7** $F_{1,15}$	**8** $F_{1,15}$	**9** $F_{1,15}$	**10** $F_{1,15}$	**11** $F_{1,15}$	**12** $F_{1,15}$	**13** $F_{1,15}$	**14** $F_{1,15}$	**15** $F_{1,15}$	**16** $F_{1,15}$	**17** $F_{1,15}$	**18** $F_{1,15}$	**19** $F_{1,15}$
sRGR	BIO	0.81	**18.4**	0.01	**10.4**	5.48	**12.0**	**15.7**	4.35	2.20	2.19	**8.04**	1.75	1.95	3.62	2.88	1.68	4.96	6.29	5.06
	Photo	0.15	0.52	0.17	5.46	0.05	4.58	4.73	0.26	3.40	0.15	1.61	10.27	0.25	0.55	0.65	0.37	0.47	0.66	0.79
	BIO × Photo	0.20	0.16	0.02	0.81	0.12	2.95	1.03	1.61	0.83	0.03	2.04	**13.3**	0.08	0.24	0.40	0.20	0.22	0.19	0.24
sNAR	BIO	0.71	**39.5**	0.41	**29.2**	**58.2**	5.38	**43.1**	2.25	**22.2**	**35.73**	3.38	1.09	1.19	5.19	4.96	0.59	**6.15**	**18.4**	**6.62**
	Photo	0.46	0.14	0.53	2.19	1.05	0.06	1.94	0.00	10.23	2.86	0.13	0.00	0.00	0.74	8.80	0.05	0.79	0.11	0.71
	BIO × Photo	2.23	1.21	2.38	1.15	1.06	2.14	1.36	0.33	**10.1**	3.07	1.14	0.00	0.01	1.16	**13.0**	0.05	1.08	0.03	1.16
sLMR	BIO	0.05	**32.5**	0.41	**10.2**	**8.12**	**8.63**	**16.2**	4.28	3.79	3.76	5.14	2.48	2.35	3.05	4.68	1.94	4.95	6.55	5.55
	Photo	1.88	5.97	5.67	3.46	1.18	0.24	5.31	2.52	0.14	11.33	1.37	0.01	0.82	0.07	0.25	0.43	0.10	0.76	0.03
	BIO × Photo	2.49	7.02	7.40	5.26	1.14	6.97	6.80	4.92	0.01	**24.1**	4.92	0.00	0.79	5.02	0.15	0.40	7.55	0.89	0.50
sSLA	BIO	0.00	**22.5**	0.16	**34.4**	**25.7**	**9.32**	**50.7**	4.35	**11.1**	**14.3**	**6.93**	0.81	1.60	4.42	2.29	0.91	5.14	**7.82**	**5.68**
	Photo	1.65	4.50	9.05	2.31	1.89	1.19	1.12	0.56	9.83	4.06	0.88	0.11	0.51	0.77	2.53	0.52	0.91	1.56	0.60
	BIO × Photo	2.07	6.61	**22.90**	0.02	1.75	0.22	0.01	0.17	8.96	3.85	0.12	0.09	0.42	2.74	2.48	0.45	2.66	1.11	2.83

Fig. S1 Comparison of alternative approaches to modelling RGR. Relationships between the different RGR measures (below the main diagonal, all g g^{-1} d^{-1}), histograms of RGR calculated using each method (diagonal), and the R^2 for relationships between RGR values calculated by alternative methods. Classical RGR was calculated as mass increase per unit of initial mass and per unit of time [RGR = ($\ln M_1$ - $\ln M_2$) / (t_2–t_1), where M_1 and M_2 are plant mass at the beginning (t_1) and end (t_2) of the vegetative growth period, respectively]. Details on the calculation of three- and four-parameter logistic RGRs can be found in Paine *et al.* (2012)[1].



[1] **Paine CET, Marthews TR, Vogt DR, Purves D, Rees M, Hector A, Turnbull LA. 2012**. How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists. *Methods in Ecology and Evolution* **3**: 245–256.

Fig. S2 Comparison of RGRs calculated at different reference sizes. Relationships between the different RGRs (below the main diagonal, all g g^{-1} d^{-1}), histograms of RGRs calculated using each reference size (diagonal), and the R^2 for relationships between RGR values calculated using alternative reference size criteria. As a common size, we used the median of the $\log_e$(mass) distribution across all focal plants, since all plants occurred at this size. As ontogenetic stages, we used the $\log_e$(mass) reached at both the inflection point (adult stage) and mid-inflection point (seedling stage) of each focal plant.

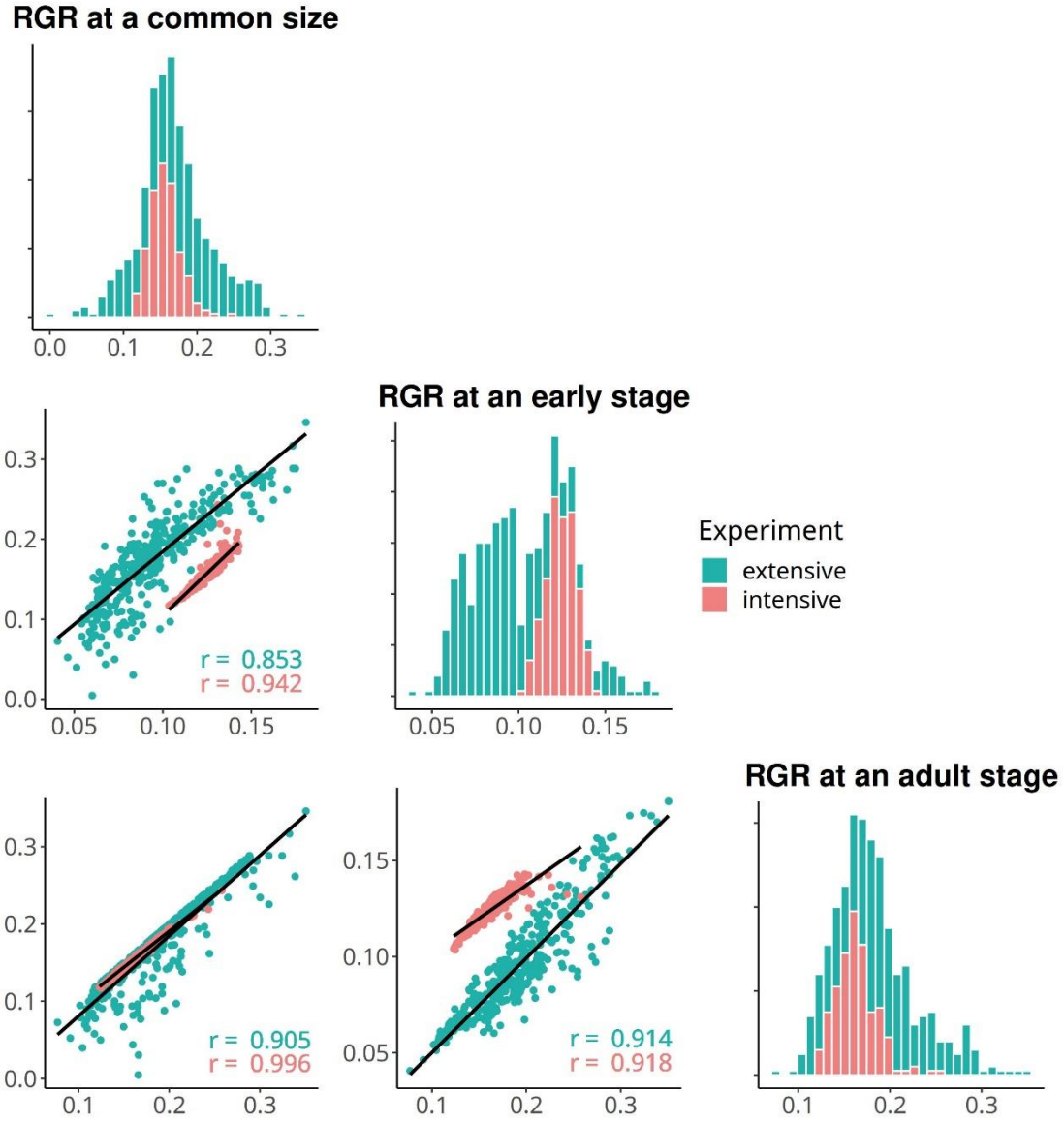


Fig. S3 Comparison of growth curve parameters in the *extensive experiment*, plotted separately by functional group: C_3 cereals, C_4 cereals, forbs and legumes, and by domestication status: wild (W), landrace (L), and improved (I) accessions. The parameters are: (a) minimum asymptote (*i.e.* the lower horizontal asymptote), (b) maximum asymptote (*i.e.* the upper horizontal asymptote), (c) steepest slope (*i.e.* the absolute increase in mass per unit time at the inflection point), and (d) arc length (*i.e.* time when the plant mass is midway between the minimum and maximum asymptotes). Boxplots show the median and 25th and 75th percentiles of the data, with whiskers extending to 1.5 times the interquartile range. Different letters denote significant differences at $P < 0.05$ after Tukey's post hoc test and false discovery rate correction.

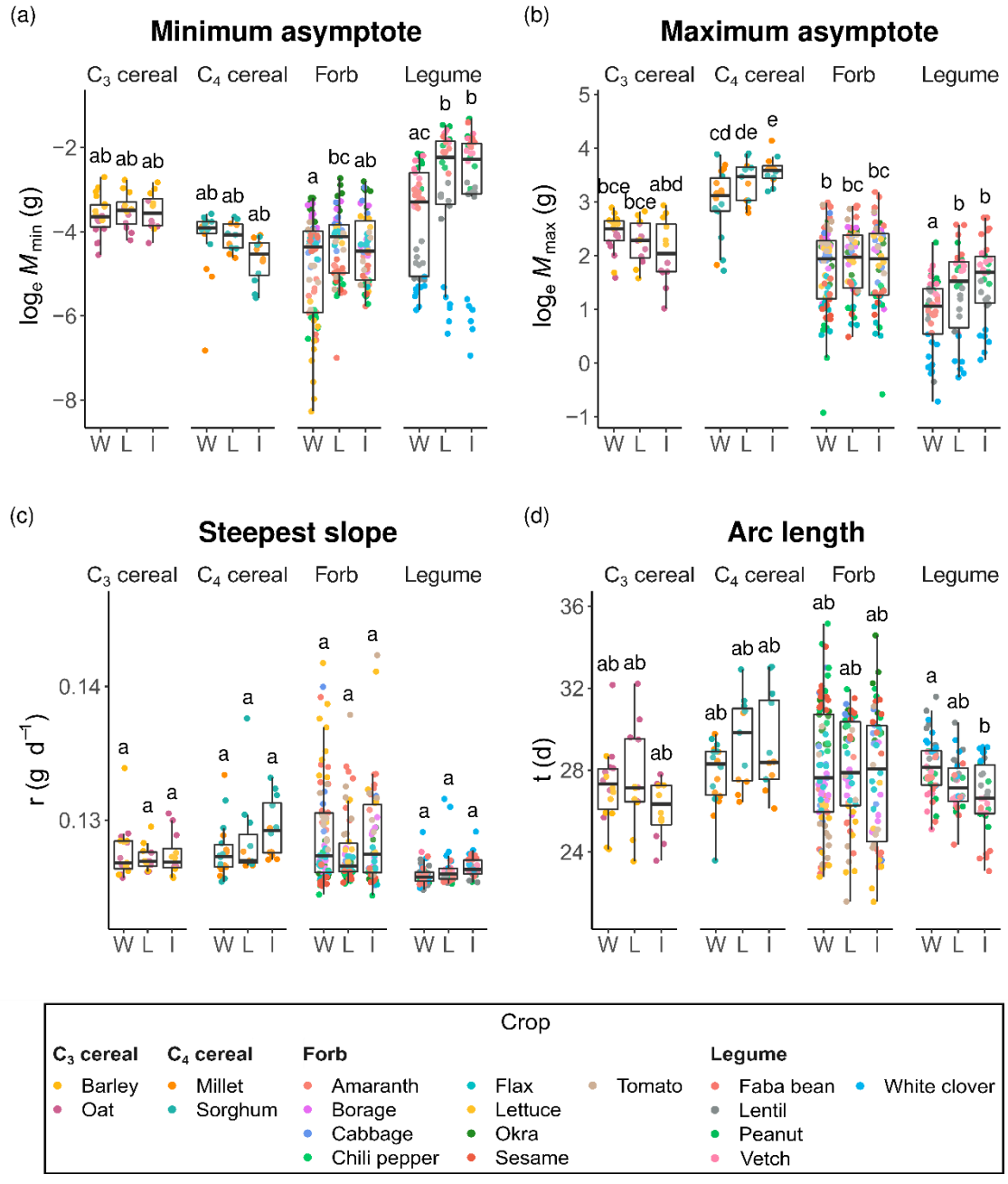


Fig. S4 Comparison of growth curve parameters in the *intensive experiment*, plotted separately by domestication status: wild (W), early landrace (EL), late landrace (LL) and improved (I) accessions. The parameters are: (a) minimum asymptote (*i.e.* the lower horizontal asymptote), (b) maximum asymptote (*i.e.* the upper horizontal asymptote), (c) steepest slope (*i.e.* the absolute increase in mass per unit time at the inflection point), and (d) arc length (*i.e.* time when the plant mass is midway between the minimum and maximum asymptotes). Boxplots show the median and 25th and 75th percentiles of the data, with whiskers extending to 1.5 times the interquartile range. Different letters denote significant differences at $P < 0.05$ after Tukey's post hoc test and false discovery rate correction.

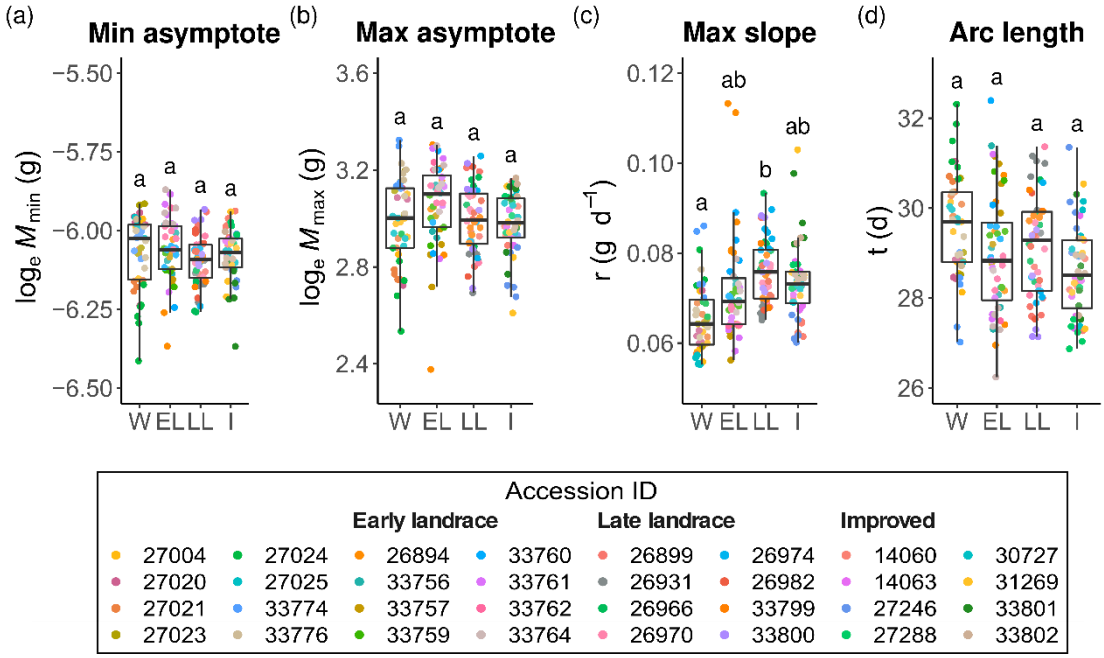
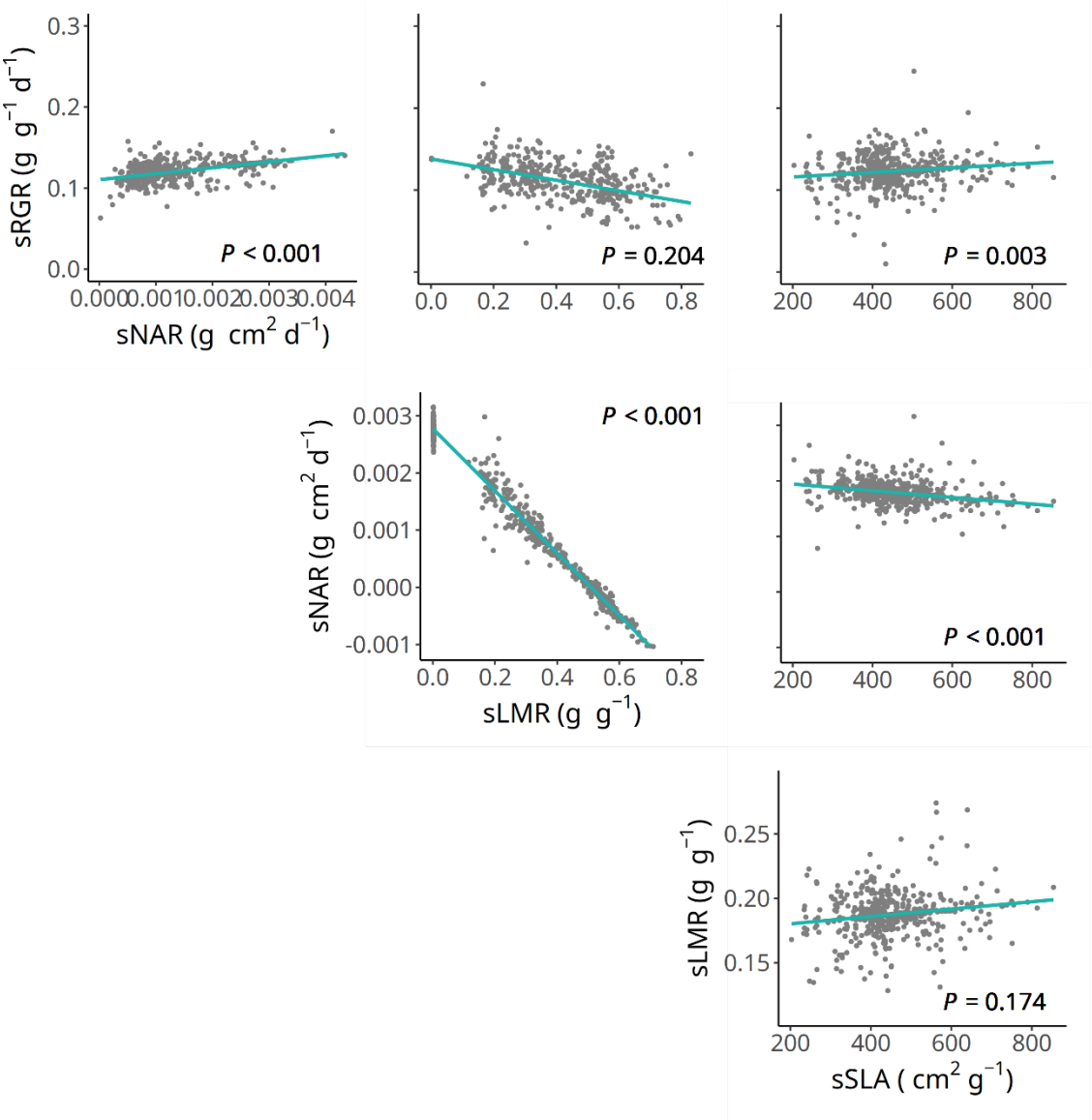


Fig. S5 Partial residuals and prediction line of the linear mixed-effects model showing the relationship between size-specific relative growth rate (sRGR), net assimilation rate (sNAR), leaf mass ratio (sLMR), and specific leaf are (sSLA). For sRGR, linear mixed-effects models included the interaction between one sRGR component, domestication status and functional group as fixed effects, and accession identity (nested within species) as random effects over the intercept. This model structure was repeated for the sRGR components as response variables. The plot was generated using the *visreg* function of the 'visreg' R package (Breheny & Burchett, 2017[2]).



[2] **Breheny P, Burchett W**. 2017. Visualization of regression models using visreg. *The R Journal* 9: 56–71.

Fig. S6 Importance of interspecific variation in size-specific net assimilation rate (sNAR), leaf mass ratio (sLMR), and specific leaf area (sSLA) to variation in size-specific relative growth rate (sRGR). Percentage variation is shown for (a) functional group: C_3 cereals, C_4 cereals, forbs, and legumes; and (b) domestication status: wild, landraces and improved cultivars, for both experiments across all percentile plant sizes.

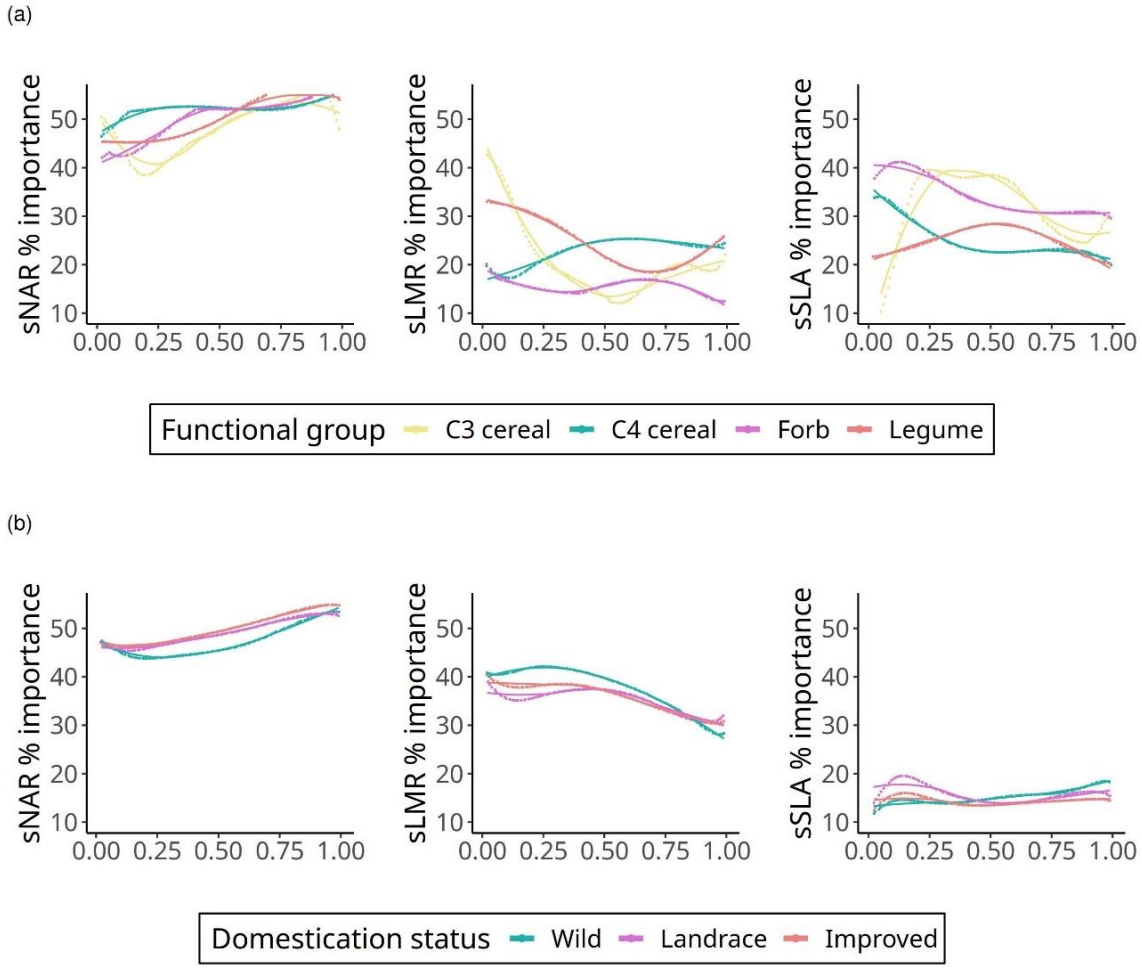
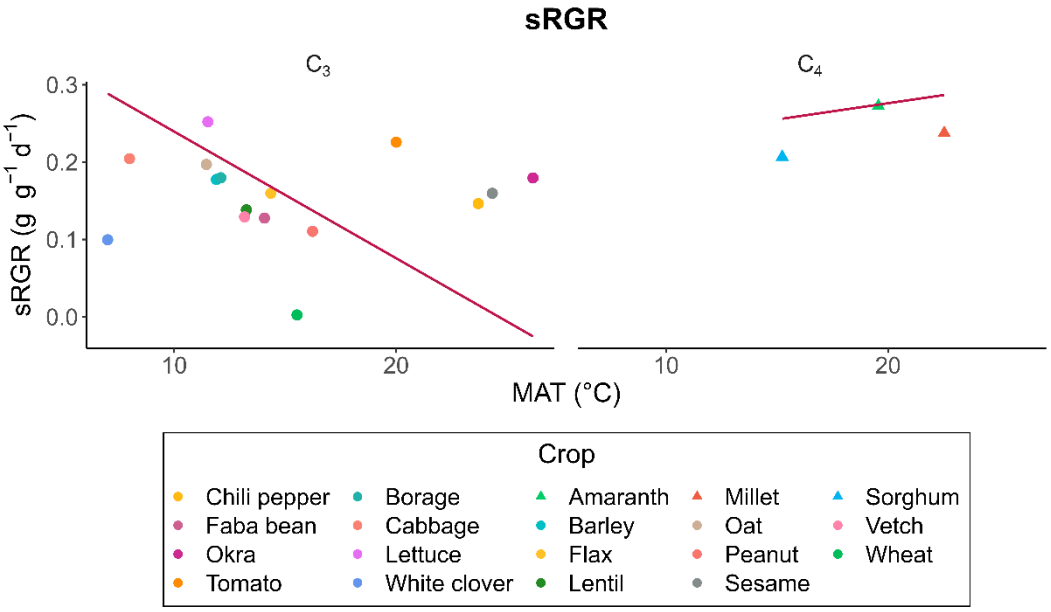


Fig. S7 Mean size-specific relative growth rate (sRGR) as a function of mean annual temperature (MAT) at crop origin and photosynthetic pathway (C_3 *vs.* C_4). Solid lines represent the fitted phylogenetic generalized least squares model (PGLS). Symbols represent the photosynthetic pathway: C_3 (circles) and C_4 (triangles).



Methods S1 Supplementary details on the estimation of total mass, leaf mass, and leaf area.

Linear regressions were performed to obtain prediction equations for total mass (lntotalM), leaf mass (lnleafM), and leaf area (lnleafA) using data from calibration plants (harvest_IN and harvest_EX for the *intensive* and *extensive experiments*, respectively). The final models for each experiment and response variable were:

INTENSIVE EXPERIMENT

1. Total mass calibration

lmer(lntotalM ~ lnheight + lncanopyd + lnleafn + time + (1 + lnheight + lncanopyd + lnleafn|acc_number), data = harvest_IN)

2. Leaf mass calibration

lmer(lnleafM ~ lnheight + lncanopyd + lnleafn + time + (1 + lnheight + lncanopyd + lnleafn|acc_number), data = harvest_IN)

3. Leaf area calibration

lmer(lnleafA ~ lntillern + lnleafn + lnleafl + time + (1 + lntillern + lnleafn + lnleafl|acc_number), data = harvest_IN)

EXTENSIVE EXPERIMENT

1. Total mass calibration

lmer(lntotalM ~ lnheight + lncanopyd + lnleafn + lnleafl + lnbasald + time + (1 + lnheight + lncanopyd + lnleafn + lnleafl + lnbasald|sps_dom), data = harvest_EX)

2. Leaf mass calibration

lmer(lnleafM ~ lnheight + lncanopyd + lnleafn + lnleafl + lnbasald + time + (1 + lnheight + lncanopyd + lnleafn + lnleafl + lnbasald|sps_dom), data = harvest_EX)

3. Leaf area calibration

lmer(lnleafA ~ lncanopyd + lntillern + lnleafn + lnleafl + lnbasald + time + (1 + lncanopyd + lntillern + lnleafn + lnleafl + lnbasald|sps_dom), data = harvest_EX)

where lnheight is plant height (cm), lncanopyd is canopy diameter (cm), lntillern is the number of branches, lnleafn is the number of leaves, lnleafl is the length of the largest leaf, lnbasald is the diameter of the basal stem, and time is the number of days from sowing to harvest. Note that 'ln' stands for $\log_e$-transformed variables. In the *intensive experiment*, accession identity (acc_number) was considered as random effects, whereas in the *extensive experiment*, a combined variable between crop identity and domestication status (sps_dom) was used. All models were run with the lmer function of the 'lme4' R package (Bates *et al.*, 2015)[3] with maximum likelihood (ML) estimation. Each of the final models was checked by plotting predicted values against observed values from the calibration plant data and calculating Pearson correlation.

[3] **Bates D, Mächler M, Bolker BM, Walker SC**. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.

Methods S2 Details on the calculation of growth traits.

Note that for calculating RGR and its components, it is more convenient to work on a logarithmic scale. Therefore, we use lowercase letters to indicate $\log_e$-transformed variables (*e.g.* $\log_e(AL)$ = al, $\log_e(RGR)$ = rgr).

CALCULATION OF sRGR.

We calculated the size-specific RGR (sRGR) from the four-parameter logistic function using the 50th percentile of the total mass distribution (m) as the common size. For this function, the sRGR for a given individual can be written as follows:

$$sRGR_i = \frac{1/scal\ (m_{min,} - m_C)(m_{max} - m_C)}{(m_{min} - m_{max})} \qquad \text{(Eqn 1)}$$

where m_{min}, m_{max}, and $scal$ are the free parameters of the function, and m_C is the common reference size. The parameters m_{min} and m_{max} are the minimum and maximum asymptotic m, respectively, and $1/scal$ is the slope at the inflection point of the curve (R function *SSfpl* in Pinheiro *et al.* (2020) [4]).

CALCULATION OF THE COMPONENTS OF sRGR

size-standardized RGR components were calculated from sRGR according to Rees *et al.* (2010)[5]. On logarithmic scales, $_s$rgr can be expressed as the sum of its components:

$$_s rgr = \ _s nar + \ _s lmr + \ _s sla \qquad \text{(Eqn 2)}$$

These components are functions of total mass (m), leaf mass (ml), and leaf area (al) as follows:

$$_s rgr = \log_e\left(\frac{1}{AL_C}\frac{dM}{dt}\right) + (ml_C - m_C) + (al_C - ml_C) \qquad \text{(Eqn 3)}$$

To calculate the contribution of each growth component to $_s rgr$, we first calculated the time (t_C) at which each focal plant reached the common reference mass (m_C) using the four-parameter logistic equation as follows:

[4] **Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RC.** 2021. nlme: linear and nonlinear mixed effects models. R package version 3.1-152.

[5] **Rees M, Osborne CP, Woodward FI, Hulme SP, Turnbull LA, Taylor SH**. 2010. Partitioning the components of relative growth rate: how important is plant size variation? *The American Naturalist* 176: E152–E161.

$$t_C = xmid - \frac{1}{1/scal} \log_e\left(-\frac{m_{max}-m_C}{m_{min}-m_C}\right) \qquad \text{(Eqn 4)}$$

where m_{min}, m_{max}, $xmid$ and $scal$ are the free parameters of the curve and m_C is the common reference size. The parameters m_{min} and m_{max} are the minimum and maximum asymptotic m, respectively, $xmid$ is the time at which m is midway between the minimum and maximum asymptotes, and $1/scal$ is the slope at the inflection point.

Second, we estimated leaf mass (ml_C) and leaf area (al_C) at the common reference size by fitting the four-parameter logistic model to ml and al. For ml_C, the logistic model is given by:

$$ml_C = ml_{min} + \frac{ml_{max}-ml_{min}}{1+ e^{(xmid-t_C)/scal}} \qquad \text{(Eqn 5)}$$

where ml_{min}, ml_{max}, $xmid$ and $scal$ are the free parameters of the curve and t_C is the time at the common reference size. The parameters ml_{min} and ml_{max} are the minimum and maximum asymptotic ml, respectively, $xmid$ is the time at which ml is midway between the minimum and maximum asymptotes, and $1/scal$ is the slope at the inflection point of the curve. For al_C, the logistic model is given by:

$$al_C = al_{min} + \frac{al_{max}-al_{min}}{1+ e^{(xmid-t_C)/scal}} \qquad \text{(Eqn 6)}$$

where al_{min}, al_{max}, $xmid$ and $scal$ are the free parameters of the curve, and t_C is the time at the common reference size. The parameters al_{min} and al_{max} are the minimum and maximum asymptotic al, respectively, $xmid$ is the time at which al is midway between the minimum and maximum asymptotes, and $1/scal$ is the slope at the inflection point of the curve.

Finally, we used the estimates of ml_C and al_C to calculate the size-standardized lmr ($_s$lmr) and sla ($_s$sla) using equation 3. The value of nar at the common mass ($_s$nar) was then estimated as $_s$rgr – $_s$lmr – $_s$sla.

CHAPTER 3

How seeds, growth and lifespan influence plant size and yield: integrating trait relationships into ontogeny

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ABSTRACT

Seed size and growth dynamics influence plant development and performance. However, we lack a mechanistic understanding of how they lead to larger and higher-yielding plants, as they have not been explicitly studied in combination and across ontogeny. Seed size and growth dynamics have evolved differently over the course of crop evolution, but whether their relationships and contributions to plant size and yield have also changed during domestication and improvement remains unclear. Here we grew wild, landrace and improved accessions of 18 phylogenetically diverse crops in a common garden. We measured seed mass, growth rate and vegetative lifespan, together with reproductive output and plant size at three developmental stages: seedling, juvenile and adult. Using path analyses, we tested causal relationships between the different traits and revealed their relative importance for variation in plant size and crop yields. Seed mass and vegetative lifespan were more important than growth rates in explaining variation in adult plant size and yield. Trait relationships did not differ between the wild, landrace and improved accessions. Crops had larger seeds but did not grow faster or for longer time spans than their wild progenitors. The traits considered accounted for the increase in final size, but not for the increase in yields during crop evolution. Our results suggest that annual herbs reach larger sizes mainly through a combination of heavier seeds and longer vegetative growth periods. Furthermore, we argue that evolution under cultivation increased plant size only through the heavy-seed causal pathway, *via* cascading effects throughout ontogeny. Selection on other traits, not explored here, may have driven the high yields of modern crops. Overall, we provide a better mechanistic understanding of the seed size-plant size axis of plant trait variation and highlight the role of vegetative lifespan in explaining diversity in adult plant sizes. Seeds, growth and lifespan are highly functionally coordinated with plant size, and we show that this coordination has changed little during crop evolution. Our findings emphasize the need to consider multi-trait relationships across ontogeny to gain insights into the evolution of plant size and crop yields.

INTRODUCTION

Body size is relevant to multiple dimensions of life. The size of an organism influences its ecological interactions and its impact on ecosystem processes and most life-history traits correlate with body size (Peters, 1983; Woodward *et al.*, 2005). In plants, large individuals compete better for available resources, are less stress tolerant and have higher resilience to disturbance (Falster & Westoby, 2003; Niklas *et al.*, 2003; Kunstler *et al.*, 2016), reflecting differences in ecological strategies (Westoby, 1998; Grime, 2001). Plant size is also critical for vital rates, as it determines seedling survival, flowering and maturation times, and reproductive output (Moles & Leishman, 2008; Westerband & Horvitz, 2015). Furthermore, size varies by orders of magnitude within and among plant species, and extensive research has attempted to explain this variation (*e.g.* (Koch *et al.*, 2004; Niklas, 2007; Vasseur *et al.*, 2012). For example, climate, soil fertility, biogeography, ecological regime shifts, growth form, and phylogeny determine plant size (McCarthy *et al.*, 2007; Moles *et al.*, 2009; Goldberg *et al.*, 2017). However, while much progress has been made in describing the role of evolutionary and ecological drivers of plant size, less is known about the proximal mechanisms that operate during ontogeny and drive variation in final plant size. Plants differ widely in their ability to acquire and allocate biomass from seedling to juvenile to adult stages (Poorter *et al.*, 2012; Dayrell *et al.*, 2018; Henn & Damschen, 2021). This is in part because the roles of different morphological, physiological, and phenological traits change during plant development. Although ontogeny is one of the most important sources of size variation, we still do not fully understand how the interplay between different traits during plant development drive variation in final plant size.

During ontogeny, at least three types of traits can explain variation in final plant size: seed size, growth rate and vegetative lifespan (Violle *et al.*, 2007). Seed mass influences the size of other organs *via* cascading effects during ontogeny (Roach & Wulff, 1987). For example, heavier seeds often germinate earlier and grow into larger seedlings with larger organs (Moles & Westoby, 2004). More biomass in leaves and roots at the seedling stage confers an early advantage in hoarding available resources, regardless of the rates of resource acquisition per unit biomass or per unit time (Kidson & Westoby, 2000). This initial size advantage potentially leads to larger leaves, stouter stems and longer and heavier roots, and thus to larger adult plants overall (Niklas, 2004). Indeed,

previous studies have found positive relationships between seed mass and seedling size at both intra- and interspecific levels (Lush & Wien, 1980; Fenner, 1983; Jakobsson & Eriksson, 2000), as well as positive scaling between organ sizes and whole plant size (West *et al.*, 1999; Price *et al.*, 2007, 2014). Also, in global analyses of functional traits, plant size and seed mass co-vary in the same axis of plant trait variation (Díaz *et al.*, 2004, 2016; Pierce *et al.*, 2014). Therefore, heavy seeds that yield larger seedlings might amplify their effect during ontogeny and grow into larger adult plants.

In addition to initial size, growth rates also contribute to variation in final plant size. High rates of biomass gain produce ever-increasing plant sizes. Growth rates are usually measured as relative growth rate (RGR, the increase in biomass per unit of pre-existing biomass and per unit time; Blackman, 1919). Plants achieve high RGRs by enhancing photosynthetic rates and/or investing more in photosynthetically active tissues (Poorter & Remkes, 1990). RGR can thus be decomposed into three underlying components reflecting photosynthetic efficiency (NAR, net assimilation rate), biomass allocation patterns (LMR, leaf mass ratio), and biomass costs of leaf area (SLA, specific leaf area) (Poorter, 1990). The interplay between the underlying components of RGR can also drive differences in final plant size (Sun & Frelich, 2011). Finally, body size also depends on the time devoted to vegetative growth. Increasing the extent of growth potentially allows even species with smaller seeds and slow growth rates to produce larger adult plants. In fact, a common assumption in life-history theories is that delayed reproduction is associated with larger plant size (Cohen, 1976; Kozłowski, 1992). For example, annual herbs that flower later tend to be larger (Bolmgren & Cowan, 2008; Sun & Frelich, 2011). Thus, the length of the growing period also contributes to variation in final plant size.

To understand the relative roles of initial size, growth rate and vegetative lifespan in shaping final plant size, we need to look at plant ontogeny and multiple trait correlations. Plant ontogeny comprises different developmental stages such as seedling, juvenile and adult individuals (Gatsuk *et al.*, 1980). However, the size of an adult plant has often been explained without considering the earlier ontogenetic stages. This approach is only appropriate if the relationships between plant traits and size do not change during ontogeny, but this is usually not the case. For example, seed mass has a stronger influence on seedling size than on adult plant size (Stanton, 1984). The

relationship between RGR and size also shifts as plants develop (Larocque & Marshall, 1993). Moreover, numerous studies have examined the trade-offs between seed mass and growth (*e.g.* Shipley & Peters, 1990; Maranon & Grubb, 1993; Gleeson & Tilman, 1994; Swanborough & Westoby, 1996; Poorter & Rose, 2005), but few have considered ontogeny when assessing these relationships (Cornelissen, 1999; Niinemets, 2006). As correlations observed at the seedling stage may differ from those observed at maturity (Mason *et al.*, 2013; Laughlin *et al.*, 2017), understanding the causes of variation in final plant size requires an ontogenetic and multivariate approach.

Comparisons between crops and their wild progenitors show that evolution under cultivation has generally increased plant size (Milla *et al.*, 2014; Milla & Matesanz, 2017). This trend parallels other changes that have also occurred during the evolution of crop species, such as seed enlargement, shifts in growth rates, shortening or lengthening of life cycles, and ultimately increases in yield (Harlan *et al.*, 1973; Meyer & Purugganan, 2013; Gómez-Fernández *et al.*, 2022). So far, however, such changes have not been linked directly or indirectly to increases in plant size. Moreover, domestication and further improvement have differentially affected these traits, as there were different selection pressures, human behaviours and rates of evolutionary change during these two evolutionary stages (Meyer & Purugganan, 2013; Abbo *et al.*, 2014). Differential selection on these traits may therefore have also disrupted the relationships between them (Milla *et al.*, 2014). For example, wild progenitors show more and stronger correlations between root and leaf traits than their domesticated counterparts (Roucou *et al.*, 2017). However, the differential effects of domestication and improvement on the drivers of plant size, yield and their relationships are still poorly understood.

Here, we aimed to disentangle the roles of seed mass, growth rates, and duration of vegetative growth as drivers of final plant size and yield in the wild progenitors, landraces and improved cultivars of 18 annual herbaceous crops. Rather than examining each trait individually, we asked how these drivers interact to explain changes in final plant size and yield through direct and indirect effects throughout ontogeny (Fig. 1). Plants were grown under common environmental conditions and assessed for size at three developmental stages: seedling, juvenile and adult. We expect that seed, growth and ontogenetic changes in plant size all interact to determine final plant size and yield. To provide general insights into the causal relationships tested, we evaluated the robustness

of the results separately for domestication and improvement stages. Specifically, we asked (i) What is the relative importance of seed mass, RGR, and growth duration to account for variation in final plant size?; (ii) Have domestication and improvement differentially impacted on the relationships between seed and growth traits and plant size?; and (iii) To what extent do crop yields depend on final plant size and its drivers?

MATERIAL AND METHODS

We grew wild, landrace and improved accessions of 18 annual herbaceous crops under common conditions. Seed mass, relative growth rate and its underlying components, and the length of the growing period were measured for a total of 377 individual plants. We also estimated the total biomass of each plant at three ontogenetic stages (seedling, juvenile and adult) and harvested its reproductive output at the fruiting stage. Using path analyses, we assessed the relative contribution of seed mass, growth rate and vegetative lifespan to plant size variation. Furthermore, we compared the results at different evolutionary stages by independently analysing domestication (wilds *vs*. landraces) and further improvement (landraces *vs*. improved cultivars). Finally, for grain and fruit crops, we investigated how variation in final plant size and its drivers impacted on crop yields.

Study system

We selected 18 taxonomically diverse herbaceous crops for our experiment (Table 1). For each crop, we obtained seed lots from three wild accessions, two landrace accessions and two improved accessions, for a total of 126 accessions (see Supporting Information Table S1 for accession identifiers and seed donors, and Milla (2020) for literature sources on wild progenitor assignment). The wild accessions (W) are the existing wild taxa that most closely represent the ancestor of the crop, while the landrace (L) and improved (I) accessions are domesticated genotypes that have been subjected to traditional agricultural practises and intensive modern breeding, respectively. Our crops belong to four functional groups: C_3 cereals (13%), C_4 cereals (13%), legumes (26%) and forbs (*i.e*. herbaceous flowering plants that are neither graminoids nor legumes; 48%), and various families: Poaceae (22%), Amaranthaceae (5.5%), Asteraceae (5.5%), Boraginaceae (5.5%), Brassicaceae (5.5%), Linaceae (5.5%), Malvaceae (5.5%), Pedaliaceae (5.5%), Solanaceae (11%) and Fabaceae (28%). Moreover, most of them are annuals and are mainly cultivated for their seeds (56%), but also for their leaves (22%) and fruits (22%).

Wild and domesticated plants were grown from May to August 2019 in the CULTIVE lab glasshouse at Universidad Rey Juan Carlos, Móstoles, Spain. The seeds of each accession were sown on peat-filled flats and germinated within 15 days after sowing. When the radicle emerged from the testa, seedlings were transplanted into 3.6 L square pots (15 × 15 × 20 cm). The pots were filled with sand and supplemented with slow-release fertiliser (5 g L^{-1} Basacote Plus 6 M, Compo, Barcelona, Spain). The experimental conditions in the glasshouse were: mean temperature ± SD = 24 ± 5°C, mean relative humidity ± SD = 57 ± 16%, and mean photosynthetically active radiation during light hours ± SD = 892 ± 204 μmol m^{-2} s^{-1}.

Experimental procedures

Growth can be followed destructively and non-destructively (Pérez-Harguindeguy *et al.*, 2013). The first method consists of harvesting plants of the same category at regular intervals. Albeit widely used, it precludes investigation at the individual plant level. The second method is to repeatedly measure different proxies of plant size on the same individual. It provides accurate information at the individual level, but no data on biomass growth. We used a mixture of both methods as follows. In the experiment, plants were divided into two groups: *focal plants* and *calibration plants*. Several proxies of plant size (listed below) were measured non-destructively in the *focal plants* at regular intervals during the period of vegetative growth. We measured the same traits in the *calibration plants*, but these plants were harvested at regular intervals to obtain leaf and whole plant dry mass, and total leaf area. Data from the *calibration plants* were used to generate prediction equations for total mass, leaf mas, and leaf area, out of non-destructive traits. The masses and leaf areas of the *focal plants* were then estimated at each monitoring date using these equations. Further details on these procedures are described in (Gómez-Fernández *et al.*, 2022).

Seeds of *focal plants* were weighed individually in a Mettler Toledo MX5 microbalance (1 μg precision; Mettler Toledo, Columbus, OH, USA). Approximately two weeks after sowing, three seedlings per accession from seeds of different weights (light, medium and heavy) were selected for the experiment. Each *focal plant* was monitored individually every three to eight days (8 times in total), more frequently during early growth. At each monitoring date, plant height, canopy diameter, number of branches, number of leaves, length of longest leaf and diameter of basal stem were measured.

Relationships between these metrics and plant biomass have been shown in previous studies (*e.g.* Tracey *et al.*, 2016)In addition, the following phenological stages were recorded: germination stage (cotyledon(s) visible), seedling stage (first true leaves visible), juvenile stage (first axillary tillers visible), vegetative adult stage (several leaves and tillers), flowering adult stage (first flower visible), fruiting adult stage (first fruit visible).

Parallelly, eight to nine destructive harvests per crop and domestication status (either wild or domesticate) were made on the *calibration plants* throughout the entire vegetative growth period. After measuring the non-destructive traits, one *calibration plant* per crop and domestication status (wild or domesticate) was harvested. Harvested plants were washed and separated into stem, leaf, root, leaf litter, and reproductive (bud, flower and fruit) fractions. The stem fraction included petioles and rachises. We scanned all leaf laminae in grayscale at a resolution of 400 dpi using an Epson Expression 10000 XL scanner (Seiko Epson Corporation, Nagano, Japan) and calculated the total leaf area per plant using Photoshop CS6 (Adobe Systems, Inc., San Jose, CA, USA). Each plant fraction was oven-dried at 60 ℃ for three days and weighed. Total mass (g) per plant was calculated by adding all mass fractions at each harvest date.

Data analyses

Due to its anomalous growth, one individual was excluded prior to data analysis. All analyses were performed in R v.4.1.2. (R Core Team, 2021).

Calibration and estimation of biomasses

Using the *calibration plant* data, we fitted linear mixed-effects models (LMM) to obtain prediction equations for total mass, leaf mass, and leaf area. Trait, mass, and area variables were ln-transformed. For each response variable (total mass, leaf mass, or leaf area), models were run with all combinations of non-destructive trait measurements and time from sowing as fixed-effects. A combined variable between crop identity and domestication status (either wild or domesticate) was included as random slope and intercept effects (see Gómez-Fernández et al., 2022) for more details on model specification). Model selection was based on the minimum AIC value. The models finally selected explained a large proportion of the variance (in total mass: R^2m = 0.90, R^2c = 0.99; in leaf mass: R^2m = 0.82, R^2c = 0.99; in leaf area: R^2m = 0.86, R^2c = 0.99). All

models were run using the *lmer* function of the 'lme4' R package (Bates *et al.*, 2015) with maximum likelihood (ML) estimation.

The prediction equations were used to estimate the total mass, leaf mass, and leaf area of the *focal plants* at each monitoring date. Duration of vegetative growth was expressed as the number of days from sowing to the appearance of the first buds and flowers. For each *focal plant*, the minimum and maximum biomass estimated during the vegetative growth period were recorded as seedling (or initial) and adult (or final) sizes. Juvenile (or intermediate) size was the biomass reached on the monitoring date closest to the midpoint of the vegetative growth period. Overall, biomass in the *focal plant* data set ranged from 0.001 to 0.49 g at the seedling stage, 0.02 to 4.07 g at the juvenile stage, and 0.13 to 66.8 g at the adult stage.

Calculation of RGR and its components

RGR can be calculated using both the conventional and the standardised approach (Pommerening & Muszta, 2016). In the conventional approach, RGR (calculated as the log of the ratio of final to initial size divided by the time interval) is not observationally independent from our response variable (*i.e*. plant size). Moreover, conventional RGR suffers from another problem – it decreases with increasing size (Poorter & Remkes, 1990). Because of this size dependence, comparisons between species with different initial sizes have often been criticised (Turnbull *et al.*, 2008). To avoid these problems, we calculated size-standardised RGR (sRGR) by fitting a growth curve for each *focal plant* and extracting RGR at a common reference size.

Specifically, we fitted a four-parameter logistic model to the increase in total plant dry mass over time using the *nlme* function of the 'nlme' R package (Pinheiro *et al.*, 2021). The four parameters A (minimum mass), B (maximum mass), t (the time at which a plant is midway between A and B) and k (a growth parameter) were allowed to vary among individuals. According to Rees et al. (2010), sRGR can be calculated using this model as follows:

$$\mathrm{sRGR} = \frac{(1/k)(A - \ln M_C)(B - \ln M_C)}{(A - B)}$$

where Mc is the common size at which sRGR is calculated. We chose the median of the mass distribution across all *focal plants* and all monitorings as the common size, since all species occurred at this size (0.383 g).

To calculate size-standardised RGR components, we also modelled individual growth curves for leaf dry mass and leaf area over time, using the four-parameter logistic model (Rees *et al.*, 2010). We then estimated leaf area and leaf mass at the time at each *focal plant* reached the common size. We used the estimates of leaf area, leaf mass and total mass at the common size to calculate size-standardised LMR (sLMR, the ratio of total dry mass allocation to the leaves at the common size) and SLA (sSLA, the ratio of total leaf area to leaf dry mass at the common size). As sRGR can be factored into its three components ($sRGR = \text{sNAR} \times \text{sLMR} \times \text{sSLA}$; Hunt, 1982), size-standardised NAR (sNAR) was then estimated as the ratio between sRGR and the product of sLMR and sSLA.

Yield and harvest index

During fruiting, the fruits or infructescences of *focal plants* were individually enclosed in organza bags (a transparent, permeable synthetic fabric) to prevent seed dispersal. We collected their reproductive output in summer 2019 (July-August). The harvested biomass was oven-dried at 60°C for three days and weighed. The dry weight of the reproductive output was considered as a proxy for yield. Harvest index was then calculated as the ratio between the yield and the sum of the estimated final plant size and yield. Since not all plants reached maturity, yield and harvest index were calculated only for those that contained fruits and mature seeds. We also excluded crops selected for their leaves (borage, cabbage, lettuce and white clover), as their reproductive output is not an indicator of their agronomic yield.

Statistical analyses

To evaluate the effects of evolution under cultivation on seed mass, sRGR, growth duration, plant sizes (*i.e.* initial, intermediate and final sizes), yield and harvest index, we ran linear mixed-effects models (LMMs) using the *lme* function in the 'nlme' R package (Pinheiro *et al.*, 2021). Models included domestication status (ordinal variable: 0 = wild progenitor; 1 = landrace; 2 = improved cultivar) and functional group (categorical variable: C_3 cereals, C_4 cereals, forbs, and legumes) as fixed effect factors and accession

identity nested within crop species as a random factor over the intercept. All mass variables were ln-transformed to improve normality. In the presence of heteroscedasticity (evaluated with Levene's test), the variance structure of the data was modelled using the 'varIdent' weights specification within the *lme* function. The significance of the fixed factors was estimated using the *anova.lme* function with sequential (type I) sums of squares in the 'nlme' R package (Pinheiro *et al.*, 2021). The amount of variance explained by the models was measured by calculating the marginal and conditional pseudo-R^2 with the r.*squaredGLMM* function from the 'MuMIn' R package (Barton, 2020). Multiple comparison tests between the levels of domestication status were performed using the *glht* function in the 'multcomp' R package and false discovery rate correction (Hothorn *et al.*, 2008).

We examined factors influencing plant size using path analysis based on previous knowledge (*i.e.* confirmatory path analysis *sensu* Shipley, 2000). An a priori model was proposed that included a complete set of direct and indirect causal relationships (Fig. 1). In this model, we considered the following expectations:

- Seedlings from big seeds tend to be larger than those from small seeds, so they are more likely to establish and compete for resources (Kidson & Westoby, 2000; Lush & Wien, 1980). Seed reserves usually continue to influence plant size up to the juvenile stage, although to a lesser extent (Cornelissen, 1999). Therefore, we hypothesised that seed mass directly increases plant size, and its effects occur in the early stages of plant development and gradually decrease across ontogeny.
- High growth rates imply that both resource acquisition and reinvestment of resources into plant tissues are rapid, allowing plants to reach high biomass in short periods of time (Poorter, 1990). We therefore expected that sRGR would also explain ontogenetic changes in plant size.
- The organs of young plants tend to be smaller than those of adult plants and these size differences increase with the duration of vegetative growth (Dosio *et al.*, 2003). Therefore, we assumed that plant size also depends on the time devoted for vegetative growth.
- Negative relationships between seed mass and RGR are well established in the literature (Shipley & Peters, 1990; Maranon & Grubb, 1993; Gleeson & Tilman, 1994; Swanborough & Westoby, 1996; Poorter & Rose, 2005, but see Paul-Victor et al.,

2010; Turnbull et al., 2012; Simpson et al., 2021). Thus, we specified a relationship between them.

- ❖ Positive scaling relationships between organs and plant sizes have been widely reported (Niklas, 2004; Falster *et al.*, 2008). We expect that seedling size may influence juvenile sizes and ultimately final plant size *via* cascading effects during ontogeny.
- ❖ Seed mass, sRGR, vegetative lifespan, and final plant size show strong phylogenetic signals (Moles *et al.*, 2005; Liu *et al.*, 2015; Atkinson *et al.*, 2016; Neto-Bradley *et al.*, 2021). In our study, functional group co-varies largely with phylogeny, as C_3 cereals, C_4 cereals, and legumes are separate clades. Thus, we inferred that functional group distinguishes between species with different functional profiles.
- ❖ Morpho, physio and phenological traits have often changed over the course of evolution under cultivation (Meyer & Purugganan, 2013), so we included a path connecting domestication status to each plant trait.

This model (later called the 'general model') was first fitted to the entire dataset. Then, to examine how initial domestication and subsequent improvement changed traits, trait interactions and their consequences for final plant size, the causal model was also fitted to the domestication (*i.e.* wild progenitors *vs*. landraces; n = 267) and improvement (*i.e.* landraces *vs*. improved cultivars, n = 213) subsets of the data. These models tested the expectation that domestication and improvement may have differentially altered seed mass, sRGR, growth duration and final plant size, as well as their relationships (Abbo *et al.*, 2014). Since the drivers and effects of sRGR may be different for each of its components (*i.e.* sNAR, sLMR, and sSLA), we also fitted the general model by replacing sRGR with its components and specifying covariations among them. Finally, we investigated whether and how variations in final plant size and other traits affect crop yields during evolution under cultivation. To this end, we extended the general model by specifying the following additional paths to crop yield. Yield increases with increasing final plant size, especially in annuals which re-allocate a fraction of their biomass at maturity to reproduction (Weiner *et al.*, 2009). Yield often decreases with vegetative lifespan, as later flowering can shorten the time to fully develop fruits and seeds (Moles & Leishman, 2008). Yield is one of the traits that has been most intensively selected for during crop evolution, with domesticated plants being higher-yielding than their wild

progenitors (Sadras, 2007). Components of yield such as seed output show phylogenetic signal (Martin, 2021). Therefore, we hypothesised that yield (i) varies with final plant size and vegetative lifespan, (ii) differs among functional groups, and (iii) has improved during evolution under cultivation.

We chose a piecewise approach for the path analyses because it allows for the inclusion of random effects in individual models (Lefcheck, 2016). All individual models that composed the path analyses were specified as explained in the first paragraph of the Statistical Analyses subsection. We ln-transformed sRGR and its components to avoid the non-linear relationships to plant size, and standardized growth duration (mean = 0, SD = 1) prior to analysis. Evolution under cultivation was included as an exogenous ordinal variable (0 = wild progenitor; 1 = landrace; 2 = improved cultivar) and functional group as an exogenous categorical variable (C_3 cereals, C_4 cereals, forbs and legumes). In the domestication model, domestication status was coded as 0 = wild progenitor and 1 = landrace, and in the improvement model as 0 = landrace and 1 = improved cultivar. Paths between RGR components were considered correlated errors rather than directed causal paths, assuming bivariate correlations among them. Models were evaluated using tests of directed separation (d-sep; Shipley, 2009), which combines the significance of independence claims into a single Fisher's C statistic. The model is considered consistent when the C statistic is not significantly different to a χ^2 distribution ($P > 0.05$). We also computed an Akaike Information Criterion (AIC) score following to know the relative support for each SEM model (Shipley 2013).

To assess the relative importance of predictor variables on final plant size and yield, we calculated the direct, indirect, and total effects using standardised path coefficients as follows (Shipley 2000). We standardised coefficients to allow direct comparisons between relationships that are measured on different scales. Direct effects were the standardised path coefficients directly linking the predictor and response variables. Indirect effects were the product of all coefficients along the paths linking predictor and response variables through at least one intermediate variable. The total effect of a predictor on the response variable was the sum of its direct and indirect effects, taking into account all paths linking these two variables. The amount of variance explained by each endogenous variable was quantified by calculating the marginal and conditional pseudo-R^2. Finally, to test how trait-trait relationships have changed during

evolution under cultivation, we performed explicit comparations between wild progenitors, landraces and improved cultivars through a multigroup analysis. This analysis determined whether the effects of each path vary by domestication status. d-separation test, Fisher's C, AIC, standardized path coefficients, pseudo-R^2, and multigroup analysis were performed with the 'piecewiseSEM' R package (Lefcheck, 2016).

RESULTS

There was considerable variation in the predictor variables across the 18 crops studied (Fig. 2). The largest-seeded crop had seeds three orders of magnitude heavier greater than the smallest-seeded crop (faba bean: 548 mg *vs*. amaranth: 0.57 mg). This includes *ca*. a quarter of the range of variation reported worldwide for this trait (Westoby *et al.*, 1992). sRGR and growth duration varied to a lesser extent, from 0.10 for peanut to 0.27 g g^{-1} day^{-1} for amaranth, and 25 for tomato to 43 days for white clover, respectively. Response variables also varied greatly among crops. Adult plant size ranged from 1.25 for white clover to 33.4 g for millet, and yield from 1.46 for lentil to 28 g for millet. In addition to interspecific variability, there was substantial ontogenetic variability in plant size within each crop (*i.e*. total biomass varied widely throughout the 55-day growth period; Fig. S1). All path models explained more than 90% and 70% of the variance in final plant size and yield, respectively, and received high statistical support, as indicated by goodness of fit metrics (Fig. 3, 4 and 5).

Evolution of traits under cultivation

Domesticates had heavier seeds, larger seedlings, juvenile and adult plants, and higher yields than their wild progenitors, regardless of their functional group (Fig. 2a, d, e, f, g; Table S2). However, there was considerable variation in the magnitude of these trends among crops, and among accessions within crops, as indicated by the high proportion of variance explained by the random part of the models (Table S2; Fig. S2). On the other hand, sRGR and its components, growth duration and harvest index did not differ between wild and domesticated plants, but did differ between functional groups for sRGR, sNAR, and sLMR (Fig. 2b, c, h; Table S2). Domestication and improvement had different effects on the traits. In particular, domestication increased seed mass, and initial, intermediate and final sizes, while modern breeding only increased yield (Fig. 2).

Relationships among seed mass, growth rate and duration, and plant size

Evolution under cultivation affected plant size through changes in plant traits (Fig. 3a). The traits considered in this study accounted for 44% of the effects of evolution under cultivation on final plant size (Fig. 3b). The larger seeds of the domesticated plants grew into larger seedlings and juvenile plants, which ultimately affected adult size (Fig. 3a). Plant traits strongly interacted with each other during ontogeny. Seed size mainly promoted larger plants in the early ontogenetic stages and growth rate and duration did so later on (Fig. 3a). Thus, large adult plants were driven directly by rapid growth and longer growing periods and indirectly by the effect of seed mass on seedling size (Fig. 3b). Heavier seeds provided slower growth rates (Fig. 3a), but we found no clear causal relationships between seed mass and sRGR components (Fig. S3a). sNAR was the component that accounted for most of the contribution of sRGR to final plant size (Fig. S3b). Overall, seed mass and growth duration explained most of the variation in final plant size (Fig. 3b).

Separate effects of domestication and improvement

The models run separately for domestication and improvement differed from the global model and from each other in the importance of the different traits in defining final plant size, but the paths did not differ in direction and statistical significance (Fig. 4). Domestication increased final plant size *via* changes in seed mass, while modern breeding slightly decreased it through negative effects on seedling size (Fig. 4a). In both models, seed mass and growth duration were the main drivers of final plant size, but during improvement sRGR became more important (Fig. 4a). The pattern of relationships between traits was very consistent among wild progenitors, landraces and improved cultivars (Fig. S4). However, size-cascading effects during ontogeny and a few effects of growth rate and duration changed in magnitude among domestication statuses (Fig. S4).

Consequences of plant size on crop yields

Evolution under cultivation increased crop yields, mainly through other factors not accounted for by our models (direct path: 0.17; Fig. 5a). Of the traits considered in this study, seed mass mediated 20.3% of the variance in yield during crop evolution. Final plant size was the most important trait for determining yield, followed by seed mass, growth duration and finally sRGR (Fig. 5b). Large plants that grew over a shorter period of time produced higher yields (Fig. 5a). The negative effects of growth duration on yield

were buffered by its indirect effects through plant size (Fig. 5a). Seed mass and sRGR increased yield indirectly through its effects on plant size during early and late ontogeny, respectively (Fig. 5a).

DISCUSSION

We found that adult plant size depends largely on the interacting effects of initial size and the rate and duration of further growth. Of the three traits considered, seed mass and growth duration were the drivers with the highest influence on final plant size, accounting for three-quarters of the variance in final size. Thus, adult plants were larger if their seeds were heavier and they had a longer vegetative lifespan. Domesticated plants showed a modest increase in final plant size, and evolution under cultivation only increased seed size and not growth rate and duration. Our results suggest that selection for heavier seeds partly underlie the increase in plant size during domestication. Furthermore, crop yields were mainly determined by final plant size, *i.e.* the larger the plant was, the higher its reproductive output. However, the traits considered in this study did not account for the increase in yields during crop evolution. Selection for other plant traits should therefore have driven the high yields of modern crops.

Proximal drivers of variation in final plant size and crop yields

Our results show that seed mass, RGR, and vegetative lifespan accounted for a large variance in final plant size. Thus, a small set of morphological, physiological and phenological traits explained most of the variation in final plant size. Vegetative biomass has been described mathematically as a function of these morpho-physio-penological traits (Violle *et al.*, 2007) and positive correlations between these functional traits and final plant size have been reported previously (*e.g.* Leishman et al., 1995; Falster & Westoby, 2005; Du & Qi, 2010; Herron et al., 2021). However, few studies have explicitly assessed the causal structure of trait interactions driving differences in final plant size, and even fewer have quantified their relative importance (Vile *et al.*, 2006; Milla & Matesanz, 2017). Moreover, these studies provided only indirect evidence, as phenological traits were not considered and proper growth experiments were not conducted. Here we find that although increased growth rate favoured the development of large plants, its relevance was lower than that of seed mass and vegetative lifespan. Milla and Matesanz (2017) also found that physiological traits such as photosynthetic rate

and SLA were less important than leaf size (a trait allometrically related to seed size (Hodgson *et al.*, 2017)) in explaining variation in aboveground size. When look at the global scale, seed mass and plant size co-vary and are orthogonal to plant resource economics (Díaz *et al.*, 2004, 2016). At that scale, orthogonality suggests that plant size is weakly correlated with growth rates (Price *et al.*, 2014). Here, we support this pattern in the context of a multivariate causal model, but also highlight the role of vegetative lifespan as a key driver of final plant size.

We show that the relative importance of morpho-physio-phenological traits as drivers of plant size changes during ontogeny. The effects of seed mass occurred at early developmental stages and gradually decreased as sRGR and growth duration became more important for plant size. The fact that trait effects change during ontogeny can make it difficult to identify causal links between traits and the strength of interactions. For example, when seed mass is not directly correlated with adult size, this is typically interpreted as evidence against its predictive value (e.g. Shipley et al., 1989; Westoby, 1998). However, most studies assessed this relationship by disregarding the possibility that the effect of seeds on intermediate sizes *via* ontogenetic cascades might be relevant to adulthood. Standardising size-dependent traits such as RGR and its components also allowed us to distinguish effects of RGR from those attributed to its dependence on size, and to analyse the relationships between growth and size across ontogeny. We found, for example, that the effects of growth on plant size, as well as the seed mass–growth trade-off, strengthened during ontogeny. We are unaware of any previous study reporting how RGR and associated trade-offs differentially modulate changes in plant size during ontogeny. Our study therefore shows that ontogeny has a high modulating effect on plant traits and their interactions, and highlights the need to consider multi-trait relationships across ontogeny, as well as the use of size-standardised measurements, to understand the evolution of plant size.

Regarding yields, our results indicate that fruit and seed production is boosted by large final plant sizes. Consistent with this, reproductive output has been found to be positively correlated with vegetative biomass in annual plants, both between and within species (Sugiyama & Bazzaz, 1998; Aarssen *et al.*, 2001; Chambers & Aarssen, 2009; Lutman *et al.*, 2011). However, we found that plant yield is driven by the same traits that determine final plant size at the end of vegetative growth in our set of annual herbaceous

crops. As with final plant size, seed mass and growth duration were the most relevant traits determining plant yield. Although both traits strongly influence reproductive output, only seed mass has changed consistently during evolution under cultivation. Growth duration and its evolution under cultivation has received less research attention (Blackman, 2017). As it is an environmentally responsive trait, a long vegetative lifespan typically confers adaptation to non-seasonal, low-disturbance environments (Gaudinier & Blackman, 2020). For example, the pressure to flower quickly decreases in agricultural environments with long growing seasons, but increases in northern regions where earlier flowering tends to improve yields (Jones *et al.*, 2008). To understand the evolutionary trajectories of phenological traits during domestication and modern breeding, further comparative studies with crops from diverse origins are needed.

The roles of domestication and improvement in promoting large plants and higher yields

We found that final plant size increased modestly from wild progenitors to domesticated plants, although this trend varied in magnitude and direction among the 18 crops studied, from large increases during early domestication, *e.g.* in faba bean, to even reductions during later improvement, *e.g.* in oat (Figs. 2, S5). Previous studies have also found a general increase in final plant size after domestication, despite differences between crops (Milla *et al.*, 2014; Turcotte *et al.*, 2014; Milla & Matesanz, 2017; Martín-Robles *et al.*, 2018). However, the proximal mechanisms leading to such post-domestic upsizing were previously unknown. Here, we show that the larger seeds of the domesticated accessions triggered a pronounced increase in plant size early in ontogeny and a more modest increase in adult plants. Physiological and phenological traits, on the other hand, did not mediate the effects of domestication on plant size, as neither growth duration nor RGR and its components changed consistently during evolution under cultivation, in line with previous studies (e.g. Evans, 1993; Meyer & Purugganan, 2013; Preece et al., 2017; Gómez-Fernández et al., 2022). Overall, our results suggest that the role of seed mass in increasing plant size may be one of the mechanisms by which large-seeded genotypes were selected during domestication.

In addition, we found that crop yields have increased over the course of evolution under cultivation. High yields are one of the most common characteristics that distinguish crops from their wild progenitors (Harlan *et al.*, 1973; Meyer & Purugganan, 2013; Preece

et al., 2017). It is noteworthy that evolution under cultivation had an effect on yield that was not accounted for by the set of traits studied here (direct effect in Fig. 5), and that changes in reproductive allocation (*i.e.* harvest index) could not explain increases in yield. This suggests that other traits, not explored in our study, may underlie the differences in yield between domesticated plants and their wild progenitors. In this regard, further traits, processes and study scales need investigation. For example, other plant traits linked to plant size and yield have also changed during evolution under cultivation, including circadian and physiological traits (Yarkhunova *et al.*, 2016), root traits and microbiome (Ehdaie *et al.*, 2010; Hamonts *et al.*, 2018), and nutrient content and stoichiometry (Delgado-Baquerizo *et al.*, 2016). Other processes and study scales have broad implications for plant growth and reproduction, including cell division and expansion (Cheniclet *et al.*, 2005; Arendt, 2007), genome size (Roddy *et al.*, 2020)and genetic control of organ and body sizes (Mizukami, 2001; Busov *et al.*, 2008). Furthermore, plant size in combination with planting density directly impacts on crop yields (Weiner & Freckleton, 2010). Therefore, further studies are needed to determine how these other traits and mechanisms may underlie the observed effects of evolution under cultivation on crop yields.

Finally, we found a high degree of functional coordination between traits, both for the whole dataset and for the domestication and improvement stages taken separately. In other words, the patterns of trait-trait relationships (*i.e.* magnitude, direction, and significance of paths) were highly consistent across wild progenitors, landraces and improved cultivars. Other studies reported varying degrees of trait coordination over the course of crop evolution (Milla *et al.*, 2014; Roucou *et al.*, 2017). However, these studies included more diverse traits (including leaf, stem and root traits) whose evolution may be more decoupled from each other (Kembel & Cahill, 2011). Since evolution under cultivation in our study only led to consistent changes in seed mass, its effects may also not have been sufficient to decouple the patterns of trait–trait relationships that existed in wild progenitors. Even so, the notion that these traits are highly coordinated despite shifts in trait means during domestication and improvement is intuitively reasonable. Large plants take longer to reach adult size, and to survive a longer juvenile period, species with a large adult size need to have (i) a high seedling survival rate, which is achieved by producing larger seeds, and later (ii) a high competitive ability, which is achieved by rapid growth rates (Moles *et al.*, 2005; Aarssen *et al.*, 2006). Therefore, we argue that the

relationships between traits that are closely linked to vital rates throughout ontogeny are too robust to be easily decoupled.

Conclusions

Previous work has identified plant traits whose variation impacts on final plant size (e.g. Violle et al., 2007). However, their relative importance remained unexplored. Here we show that seed mass and vegetative lifespan are the main drivers of variation in final plant size. Our results therefore provide a better mechanistic understanding of the plant size - seed size axis of plant trait variation and also highlight the role of vegetative lifespan in varying final plant size. Furthermore, our results suggest that seed mass, growth rate and vegetative lifespan exhibit a high degree of functional coordination with plant size and that ontogeny plays an important role in modulating the effects of each trait.

In our study, linking plant size to the mechanisms outlined here sheds more light on why large seeds were valuable for agriculturalists. However, this trait alone did not explain the yield differences between domesticated plants and their wild progenitors. Further studies that (i) examine other plant traits, processes and study scales, and (ii) consider multi-trait relationships across ontogeny, as well as the use of size-standardised measurements, are needed to strengthen our mechanistic understanding of the evolution of crop yields.

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FIGURES

Fig. 1 Conceptual framework for exploring the effects of evolution under cultivation on factors influencing variation in plant size and yield. Seed size, growth rate and vegetative lifespan are interrelated and together determine plant size during ontogeny. Ontogeny is the development of plants at different stages (seedling, juvenile and adult). Growth rate is the relative growth rate (RGR) and its underlying components (*i.e*. net assimilation rate (NAR), leaf mass ratio (LMR) and specific leaf area (SLA)). Due to positive scaling, yield should increase with the increase in adult plant size.

Fig. 2 Trait variation by domestication status (W = wild progenitor; L = landrace; I = improved cultivar). Boxplots show the median and 25th and 75th percentiles of the data, with whiskers extending to 1.5 times the interquartile range. Colours represent different crop species and symbols are functional groups: C_3 cereals (diamonds), C_4 cereals (circles), forbs (triangles) and legumes (squares). Different letters indicate significant differences at $P < 0.05$ after Tukey's post hoc test and false discovery rate correction. Abbreviations: seed size, seed mass; sRGR, size-standardised relative growth rate; growth duration, vegetative lifespan; initial size, dry biomass at the seedling stage; intermediate size, dry biomass at the juvenile stage; final size, dry biomass at the adult stage; yield, dry reproductive biomass for seed and fruit crops; harvest index, the ratio of yield to total dry biomass at the mature stage.

Fig. 3 (a) Path diagram of relationships between seed size, growth rate and duration, and plant size. Evolution under cultivation was included as an exogenous ordinal variable (0 = wild progenitor; 1 = landrace; 2 = improved cultivar) and functional group as an exogenous categorical variable (C_3 cereals, C_4 cereals, forbs and legumes). Solid arrows (→) are positive effects and dashed arrows (⇢) are negative effects. Arrow widths are proportional to the magnitude of the standardized path coefficients (indicated by the numbers on the lines). All path coefficients are significantly different from zero at $P < 0.05$ unless 'n.s.' (not significant) is indicated. Marginal (R^2m) and conditional (R^2c) pseudo-R^2 are the proportion of variance in mature plant size explained by fixed effects and all effects (fixed plus random effects), respectively. The global model fit the data (Fisher's C = 13.62, d.f. = 10, $P = 0.191$, N = 377). For trait abbreviations see Fig. 2. (b) Synthesis of direct, indirect, and total effects of evolution under cultivation, seed size,

sRGR, and growth duration on mature plant size, derived from (a). Direct effects (D) are the standardized path coefficients directly linking mature plant size to the predictor variables. Indirect effects (I) are the product of coefficients along paths linking mature plant size to predictors through at least one intermediate variable. The total effect (T) of a predictor on mature plant size is the sum of its direct and indirect effects (Shipley, 2000).

Fig. 4 (a) Path diagram of relationships between seed size, growth rate and duration, and plant size for domestication (top) and improvement (bottom). Domestication and improvement were included as exogenous ordinal variables (domestication: 0 = wild progenitor; 1 = landrace; improvement: 0 = landrace; 1 = improved cultivar) and functional group as an exogenous categorical variable (C_3 cereals, C_4 cereals, forbs, and legumes). The meanings of path coefficients, line styles, arrow widths, and pseudo-R^2 are the same as in Fig. 3. The global model fit the data (in the domestication model: Fisher's C = 10.09, d.f. = 10, P = 0.433, N = 269; in the improvement model: Fisher's C = 16.27, d.f. = 10, P = 0.092, N = 215). For trait abbreviations see Fig. 2. (b) Synthesis of direct, indirect, and total effects of domestication/improvement, seed size, sRGR, and growth duration on adult plant size, derived from (a). The meaning of the direct (D), indirect (I), and total effects (T) is the same as in Fig. 3.

Fig. 5 (a) Path diagram of relationships between seed size, growth rate and duration, plant size, and yield. Evolution under cultivation was included as an exogenous ordinal variable (0 = wild progenitor; 1 = landrace; 2 = improved cultivar) and functional group as an exogenous categorical variable (C_3 cereals, C_4 cereals, forbs and legumes). The meanings of path coefficients, line styles, arrow widths, and pseudo-R^2 are the same as in Fig. 3. The global model fit the data (Fisher's C = 24.24, d.f. = 18, P = 0.147, N = 206). For trait abbreviations see Fig. 2. (b) Synthesis of direct, indirect, and total effects of evolution under cultivation, seed size, sRGR, growth duration, and mature plant size on yield derived from (a). Direct effects (D) are the standardized path coefficients directly linking yield to the predictor variables. Indirect effects (I) are the product of coefficients along paths linking yield to predictors through at least one intermediate variable. The total effect (T) of a predictor on yield is the sum of its direct and indirect effects (Shipley, 2000).

Fig. 1

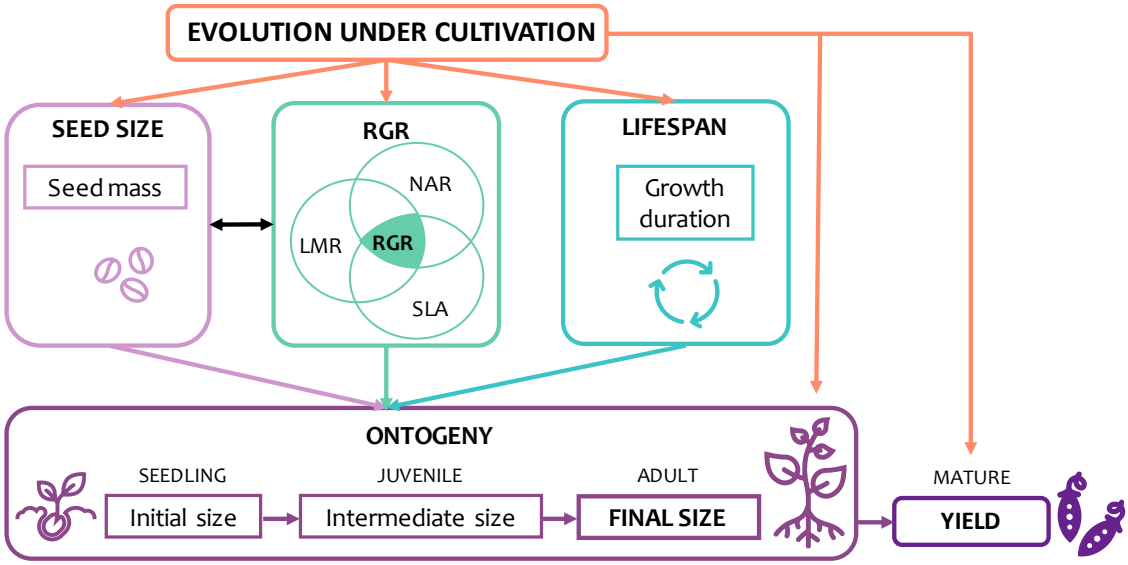

EVOLUTION UNDER CULTIVATION
SEED SIZE
Seed mass
RGR
NAR
LMR
RGR
SLA
LIFESPAN
Growth duration
ONTOGENY
SEEDLING
Initial size
JUVENILE
Intermediate size
ADULT
FINAL SIZE
MATURE
YIELD

Fig. 2

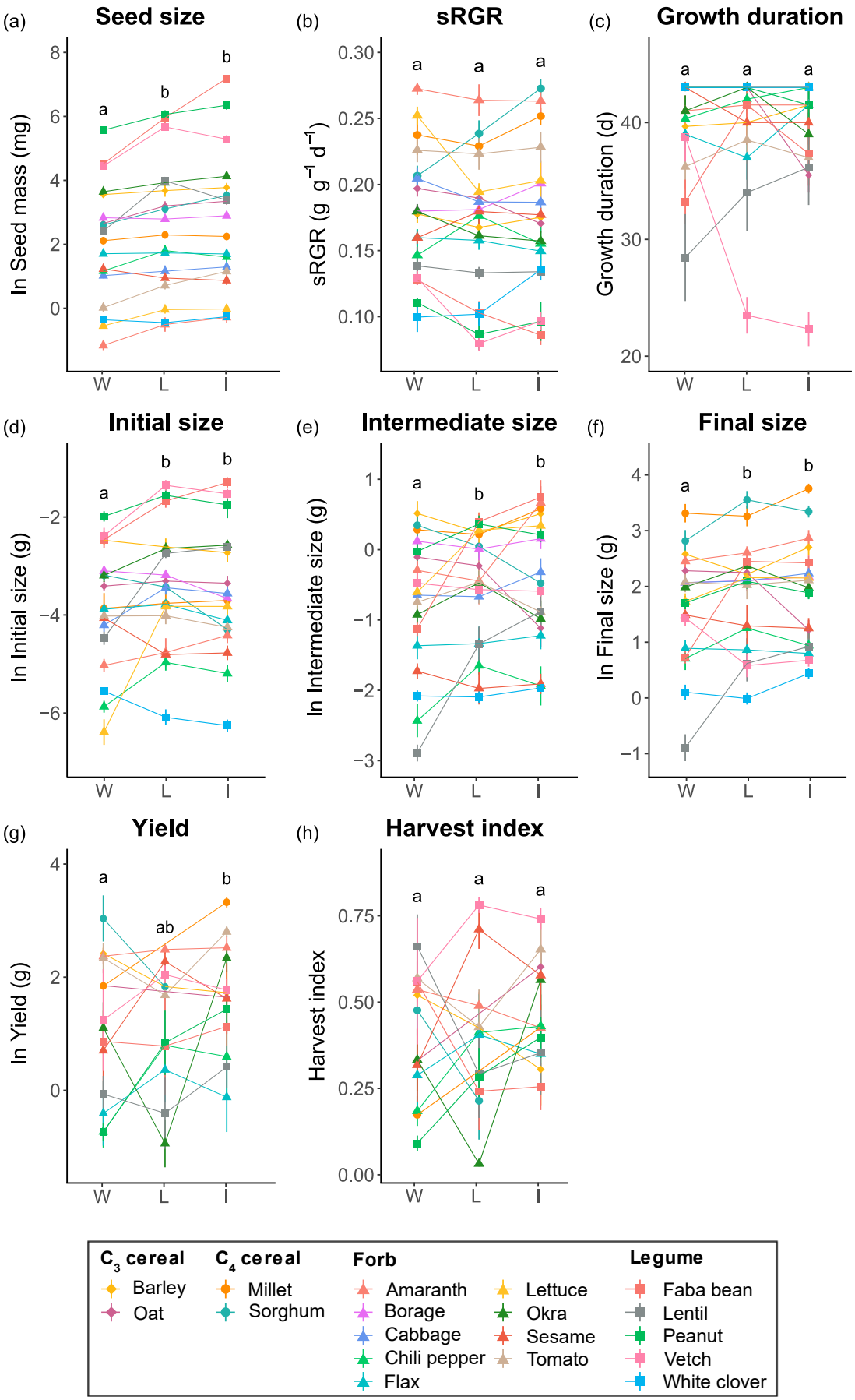

(a)
Seed size
ln Seed mass (mg)
(b)
sRGR
sRGR (g g⁻¹ d⁻¹)
(c)
Growth duration
Growth duration (d)
(d)
Initial size
ln Initial size (g)
(e)
Intermediate size
ln Intermediate size (g)
(f)
Final size
ln Final size (g)
(g)
Yield
ln Yield (g)
(h)
Harvest index
Harvest index
W
L
I
C3 cereal
Barley
Oat
C4 cereal
Millet
Sorghum
Forb
Amaranth
Borage
Cabbage
Chili pepper
Flax
Lettuce
Okra
Sesame
Tomato
Legume
Faba bean
Lentil
Peanut
Vetch
White clover

Fig. 3

(a) (b)

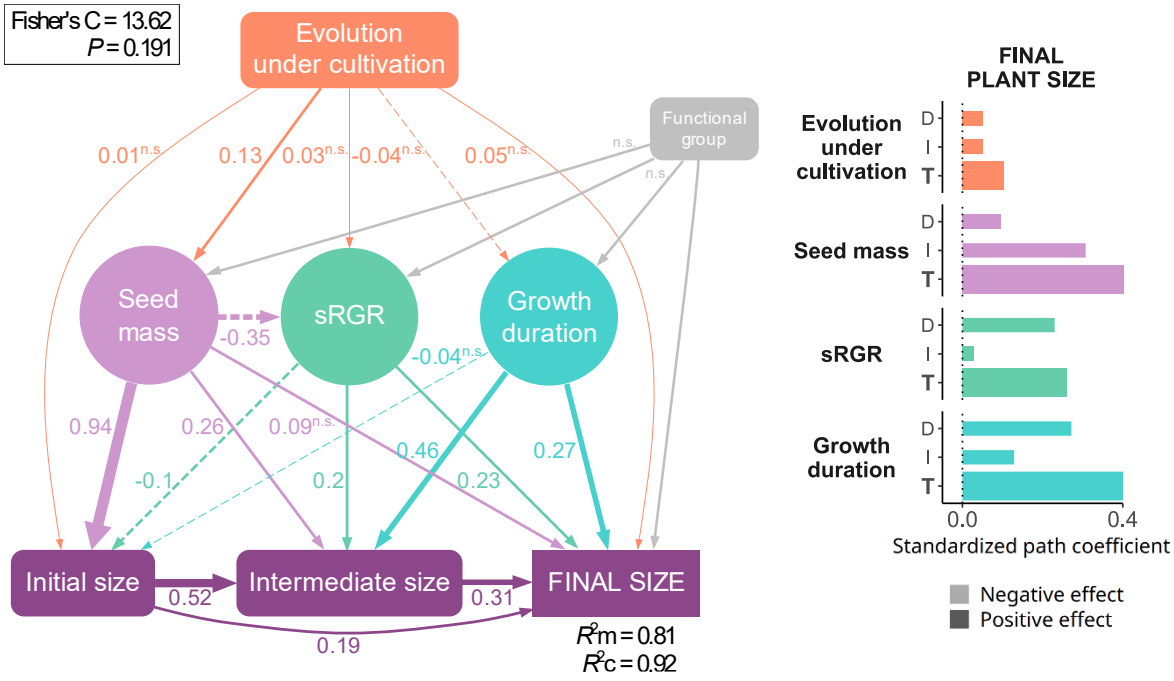

Fisher's C = 13.62
P = 0.191
Evolution under cultivation
Functional group
Seed mass
sRGR
Growth duration
Initial size
Intermediate size
FINAL SIZE
0.01n.s.
0.13
0.03n.s.
-0.04n.s.
0.05n.s.
n.s.
n.s.
-0.35
-0.04n.s.
0.94
0.26
0.09n.s.
0.46
0.27
-0.1
0.2
0.23
0.52
0.31
0.19
R2m = 0.81
R2c = 0.92
FINAL PLANT SIZE
Evolution under cultivation
Seed mass
sRGR
Growth duration
D
I
T
0.0
0.4
Standardized path coefficient
Negative effect
Positive effect

Fig. 4

(a) (b)

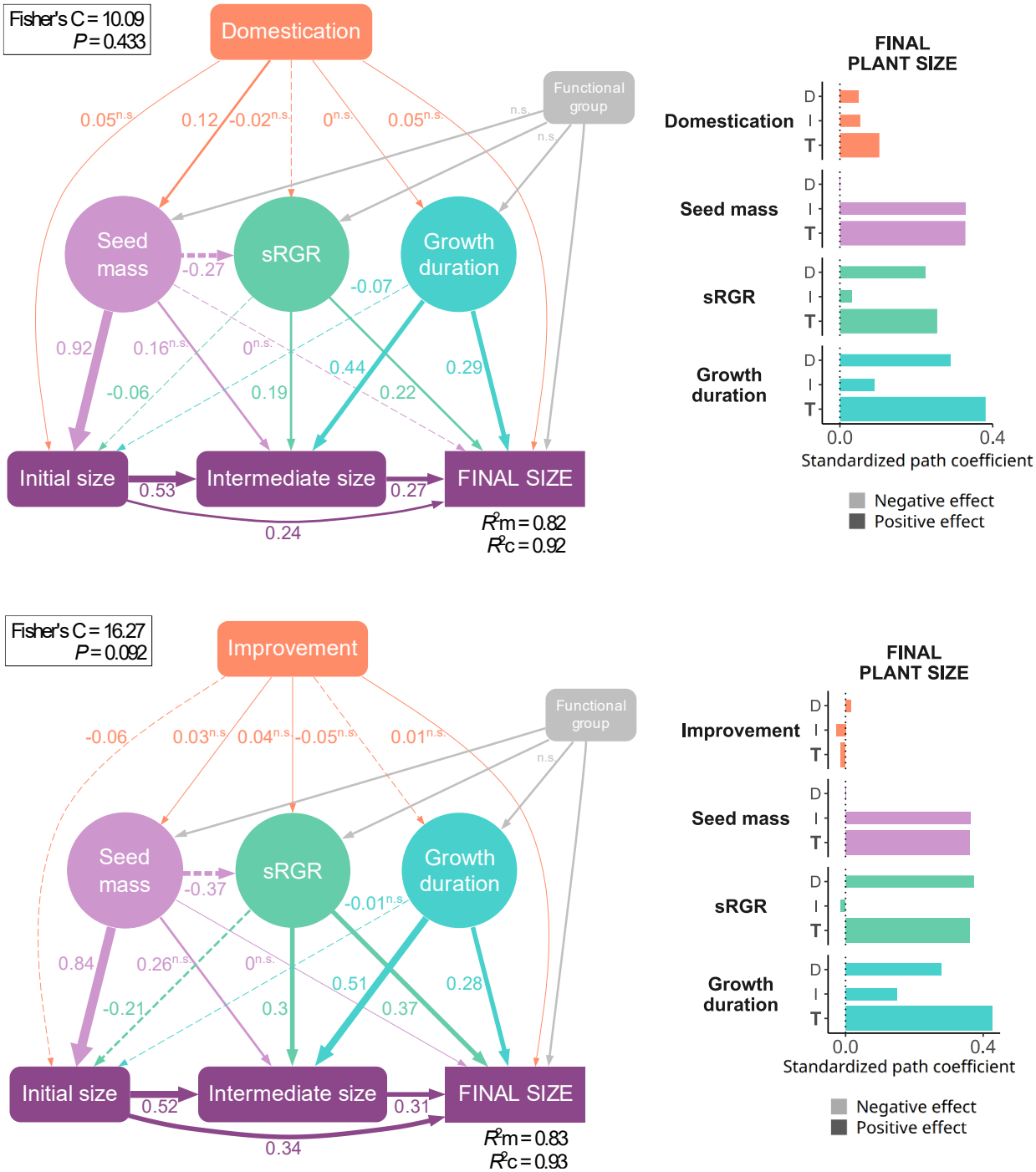
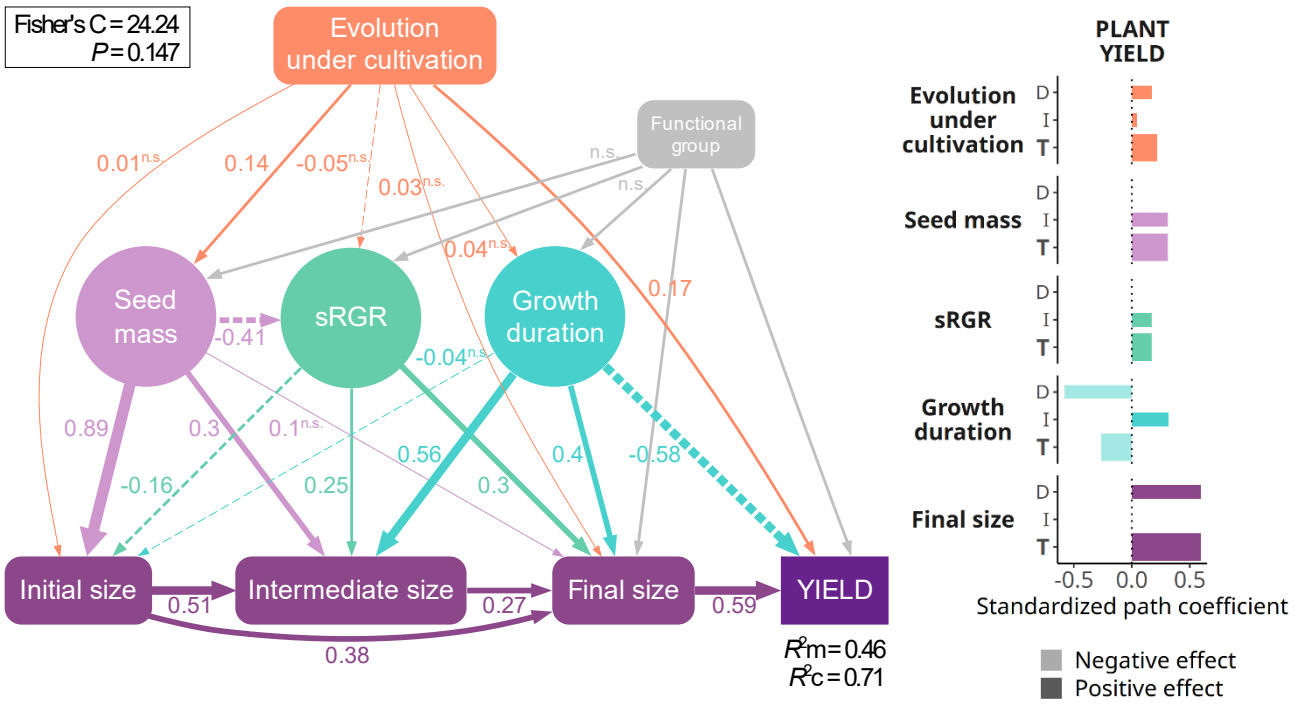

Fisher's C = 10.09
P = 0.433
Domestication
Functional group
Seed mass
sRGR
Growth duration
Initial size
Intermediate size
FINAL SIZE
0.05n.s.
0.12
-0.02n.s.
0n.s.
0.05n.s.
n.s.
n.s.
-0.27
-0.07
0.92
0.16n.s.
0n.s.
0.44
0.29
-0.06
0.19
0.22
0.53
0.27
0.24
R2m = 0.82
R2c = 0.92
FINAL PLANT SIZE
Domestication
Seed mass
sRGR
Growth duration
D
I
T
0.0
0.4
Standardized path coefficient
Negative effect
Positive effect
Fisher's C = 16.27
P = 0.092
Improvement
Functional group
Seed mass
sRGR
Growth duration
Initial size
Intermediate size
FINAL SIZE
-0.06
0.03n.s.
0.04n.s.
-0.05n.s.
0.01n.s.
n.s.
-0.37
-0.01n.s.
0.84
0.26n.s.
0n.s.
0.51
0.28
-0.21
0.3
0.37
0.52
0.31
0.34
R2m = 0.83
R2c = 0.93
FINAL PLANT SIZE
Improvement
Seed mass
sRGR
Growth duration
D
I
T
0.0
0.4
Standardized path coefficient
Negative effect
Positive effect

Fig. 5

(a) (b)


Fisher's C = 24.24
P = 0.147
Evolution under cultivation
Functional group
Seed mass
sRGR
Growth duration
Initial size
Intermediate size
Final size
YIELD
0.01n.s.
0.14
-0.05n.s.
0.03n.s.
n.s
n.s
0.04n.s.
0.17
-0.41
-0.04n.s.
0.89
0.3
0.1n.s.
0.56
0.4
-0.58
-0.16
0.25
0.3
0.51
0.27
0.59
0.38
R2m = 0.46
R2c = 0.71
PLANT YIELD
Evolution under cultivation
Seed mass
sRGR
Growth duration
Final size
D
I
T
-0.5
0.0
0.5
Standardized path coefficient
Negative effect
Positive effect

TABLES

TABLE 1 Common and botanical names of the wild and domesticated taxa of each of the 18 crops used in the experiment, as well as their functional group affiliations. Domesticated plants refer to accessions belonging to both landraces and improved cultivars.

Common name	**Wild progenitor**	**Domesticated plant**	**Functional group**
Barley	*Hordeum spontaneum* K.Koch	*Hordeum vulgare* L.	C_3 cereal
Oat	*Avena sterilis* L.	*Avena sativa* L.	C_3 cereal
Pearl millet	*Pennisetum glaucum* (L.) R.Br.	*Pennisetum glaucum* (L.) R.Br.	C_4 cereal
Sorghum	*Sorghum arundinaceum* (Desv.) Stapf	*Sorghum bicolor* (L.) Moench	C_4 cereal
Amaranth	*Amaranthus hybridus* L.	*Amaranthus cruentus* L.	Forb
Lettuce	*Lactuca serriola* L.	*Lactuca sativa* L.	Forb
Borage	*Borago officinalis* L.	*Borago officinalis* L.	Forb
Cabbage	*Brassica oleracea* L.	*Brassica oleracea* L.	Forb
Flax	*Linum usitatissimum* L.	*Linum usitatissimum* L.	Forb
Okra	*Abelmoschus tuberculatus* Pal & Singh	*Abelmoschus esculentus* (L.) Moench	Forb
Sesame	*Sesamum indicum* L.	*Sesamum indicum* L.	Forb
Chili pepper	*Capsicum baccatum* L.	*Capsicum baccatum* L.	Forb
Tomato	*Solanum pimpinellifolium* L.	*Solanum lycopersicum* L.	Forb
Faba bean	*Vicia narbonensis* L.	*Vicia faba* L.	Legume
Lentil	*Lens culinaris* ssp. *orientalis* (Boiss.) Ponert	*Lens culinaris* Medik.	Legume
Peanut	*Arachis monticola* Krapov. & Rigoni	*Arachis hypogaea* L.	Legume
Vetch	*Lathyrus cicera* L.	*Lathyrus sativus* L.	Legume
White clover	*Trifolium repens* L.	*Trifolium repens* L.	Legume

SUPPORTING INFORMATION

Fig. S1 Total biomass of individuals for each of the 18 crops included in the experiment over a 55-day growth period. Curves represent the fitted four-parameter logistic model for each crop species. Colours indicate domestication status: blue, wild progenitors; purple, landraces; green, improved cultivars.

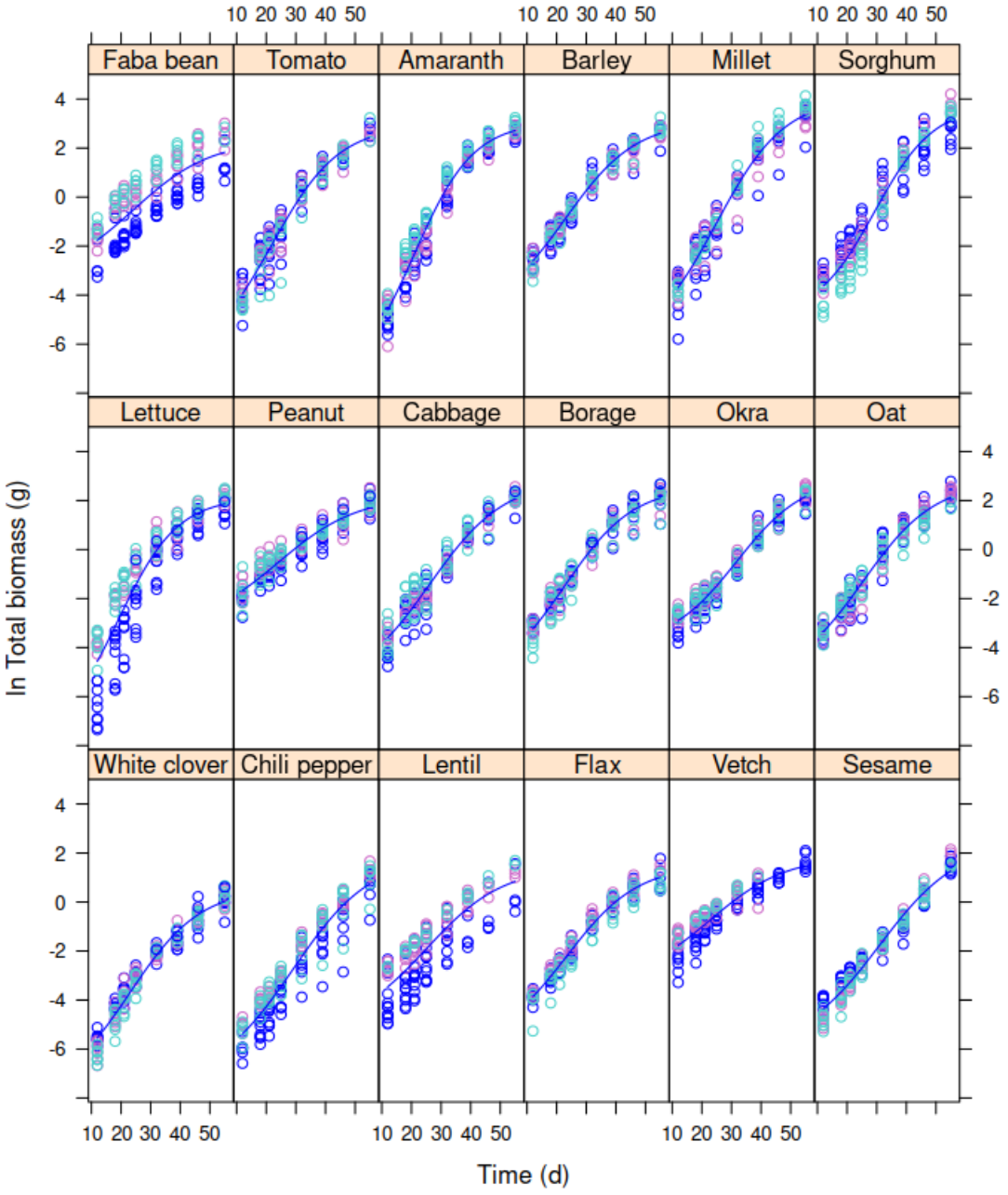


Fig. S2 Changes in plant traits during evolution under cultivation in the 19 crops studied. The dots are the effect sizes estimated by Hedges' *G*, and the bars are the 95% confidence intervals. Negative scores of Hedges' *G* indicate negative effects of evolution under cultivation on seed size, size-specific relative growth rate (sRGR), growth duration, initial and final sizes, and yield, and vice versa for positive scores. Colours indicate functional group affiliation: C_3 cereals (yellow), C_4 cereals (blue), forbs (pink), and legumes (red).

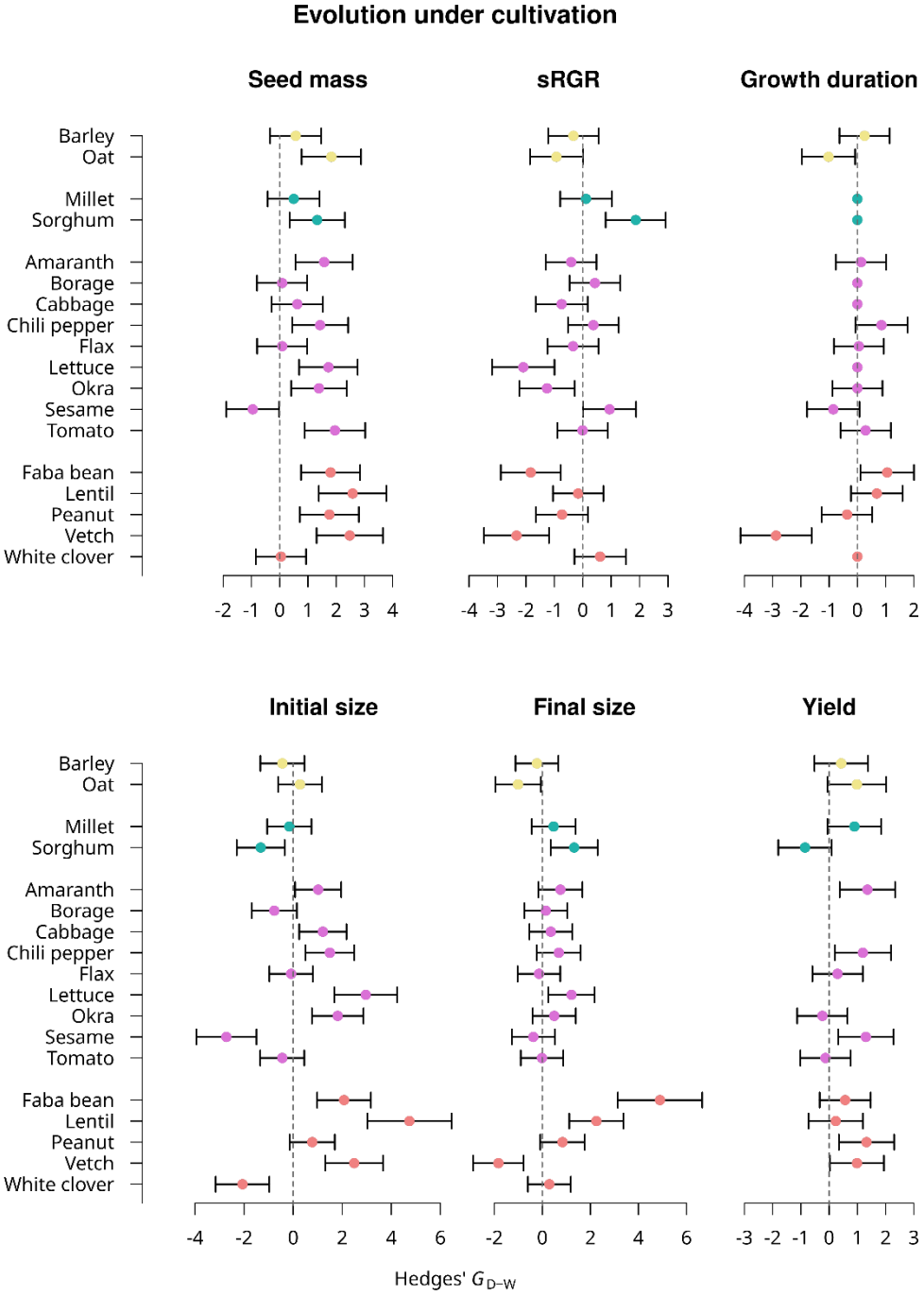
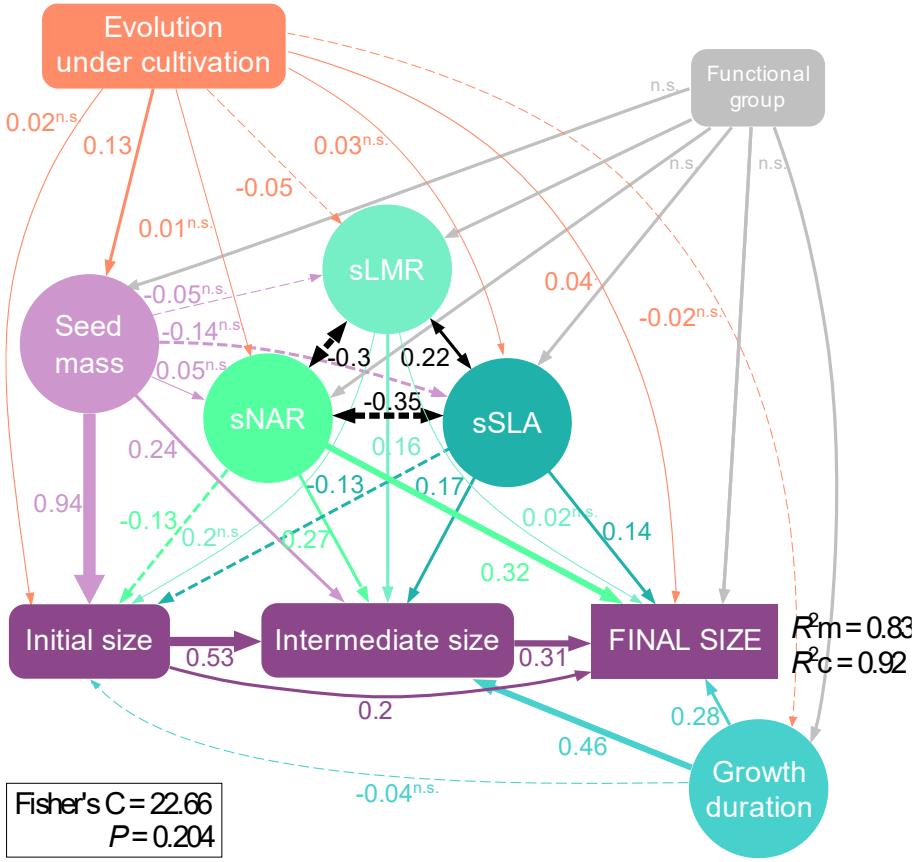


Fig. S3 (a) Path diagram of relationships between seed size, growth rate and duration, and plant size. Evolution under cultivation was included as an exogenous ordinal variable (0 = wild progenitor; 1 = landrace; 2 = improved cultivar) and functional group as an exogenous categorical variable (C_3 cereals, C_4 cereals, forbs, and legumes). Solid arrows (→) are positive effects and dashed arrows (⇢) are negative effects. Arrow widths are proportional to the magnitude of the standardized path coefficients (indicated by the numbers on the lines). All path coefficients are significantly different from zero at $P < 0.05$ unless 'n.s.' (not significant) is indicated. Marginal (R^2m) and conditional (R^2c) pseudo-R2 are the proportion of variance in final plant size explained by fixed effects and all effects (fixed plus random effects), respectively. The global model fit the data (Fisher's C = 22.66, d.f. = 18, $P = 0.204$, N = 377). Abbreviations: sNAR, size-specific net assimilation rate; sLMR, size-specific leaf mass ratio; sSLA, size-specific specific leaf area. (b) Synthesis of direct, indirect, and total effects of evolution under cultivation, seed size, sNAR, sLMR, sSLA, and growth duration on final plant size, derived from (a). Direct effects (D) are the standardized path coefficients directly linking final plant size to the predictor variables. Indirect effects (I) are the product of coefficients along paths linking final plant size to predictors through at least one intermediate variable. The total effect (T) of a predictor on final plant size is the sum of its direct and indirect effects (Shipley, 2000).

(a)


Evolution under cultivation
Functional group
Seed mass
sLMR
sNAR
sSLA
Initial size
Intermediate size
FINAL SIZE
Growth duration
0.02n.s.
0.13
0.03n.s.
-0.05
0.01n.s.
n.s.
n.s.
n.s.
-0.05n.s.
-0.14n.s.
0.05n.s.
0.04
-0.02n.s.
-0.3
0.22
-0.35
0.24
0.16
0.94
-0.13
0.17
-0.13
0.2n.s.
0.27
0.02n.s.
0.14
0.32
0.53
0.31
0.2
0.28
0.46
-0.04n.s.
R2m = 0.83
R2c = 0.92
Fisher's C = 22.66
P = 0.204

(b)

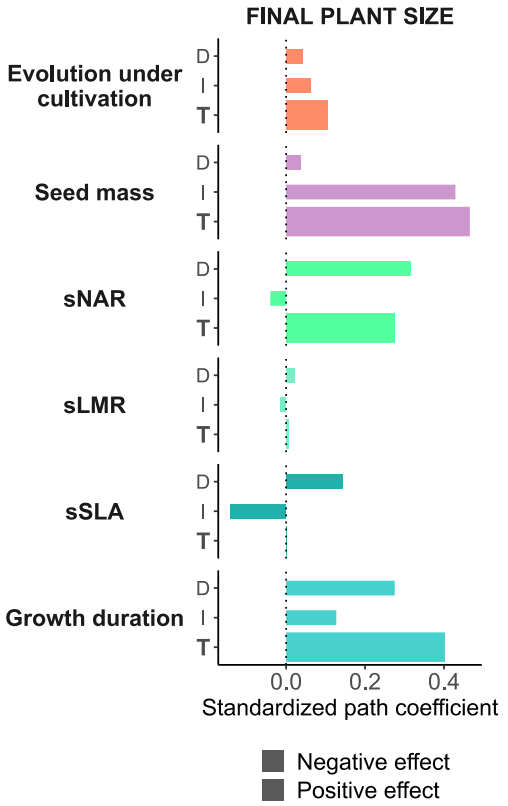

FINAL PLANT SIZE
Evolution under cultivation
Seed mass
sNAR
sLMR
sSLA
Growth duration
D
I
T
0.0
0.2
0.4
Standardized path coefficient
Negative effect
Positive effect

Fig. S4 Results of multigroup path analysis showing the seed-growth-size relationships between (a) wild progenitors, (b) landraces and (c) improved cultivars. Functional group was included as an exogenous categorical variable (C3 cereals, C4 cereals, forbs, and legumes). Black lines denote the paths constrained to be significantly equal between groups. Solid arrows (→) are positive effects and dashed arrows (⇢) are negative effects. Arrow widths are proportional to the magnitude of the standardized path coefficients (indicated by the numbers on the lines). All path coefficients are significantly different from zero at $P < 0.05$ unless 'n.s.' (not significant) is indicated. The global model fit the data (Fisher's C = 14.06, d.f. = 8, $P = 0.08$, N = 377 (162 wilds, 107 landraces, 108 cultivars)). * For analytical reasons, the differences between the functional groups in growth duration could not be evaluated. Abbreviations: sRGR, size-specific relative growth rate.

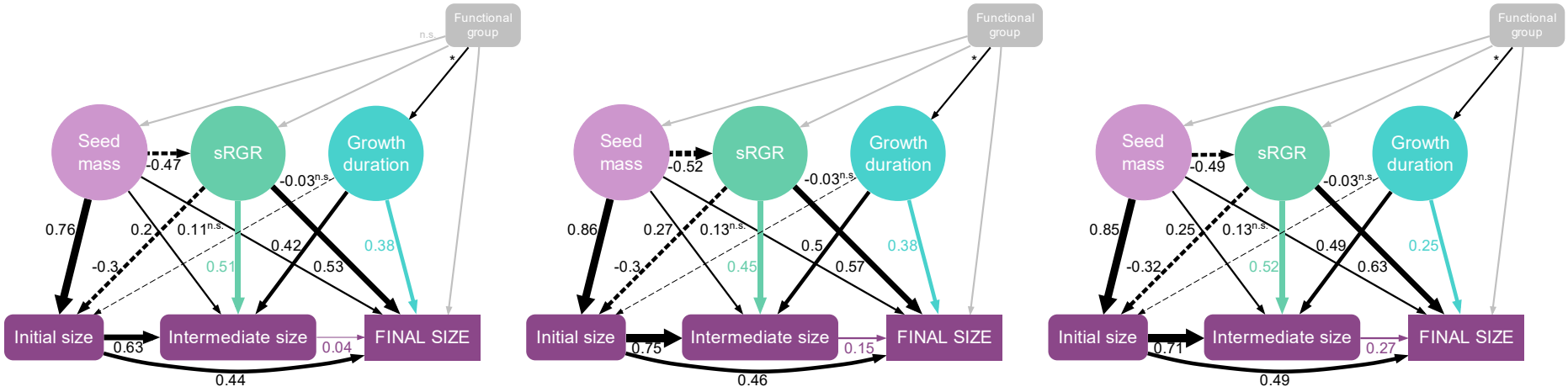


Fig. S5 Changes in final plant size during (a) domestication and (b) improvement of the 18 crops studied. The dots are the effect sizes estimated by Hedges' G, and the bars are the 95% confidence intervals. Negative scores of Hedges' G indicate negative effects of domestication or improvement on final plant size, and vice versa for positive scores. Colours indicate functional group affiliation: yellow, C_3 cereals; blue, C_4 cereals; pink, forbs; red, legumes.

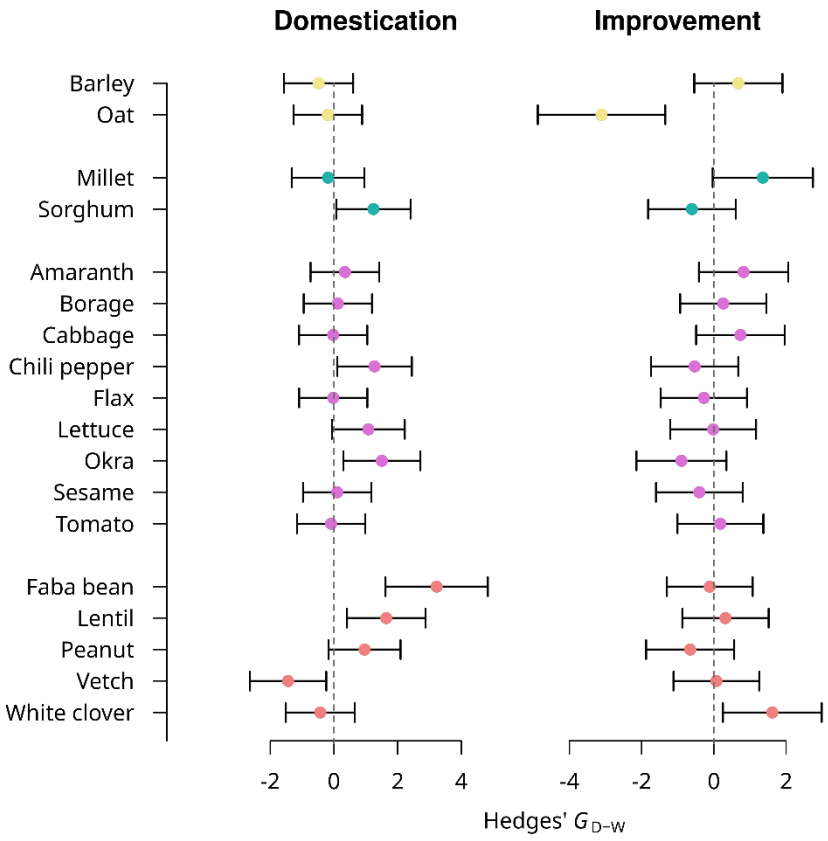


Table S1 Common and botanical names, family, domestication status and seed origin information for each accession used in the experiment. Accession identifier refers to the code assigned by each seed donor, with the exception of commercial companies (N.A. = not applicable). Accession country refers to the country where seeds were originally collected, if applicable. Seed donor (BGVCU: Banco de Germoplasma Vegetal de Cuenca, Spain; CGN: Center for Genetic Resources, The Netherlands; CITA: Centro de Investigación y Transferencia Agroalimentaria de Aragón, Spain; COMAV: Instituto Universitario de Conservación y Mejora de la Agrodiversidad Valenciana, Spain; CRF: Centro Nacional de Recursos Fitogenéticos-INIA, Spain; ICARDA: International Center for Agricultural Research in Dry Areas, Syria; IPK: Germplasm bank of the Leibniz Institute of Plant Genetics and Crop Plant Research, Germany; NPGS: National Plant Germplasm System-USDA, U.S.A.; *: commercial company).

Common name	Family	Botanical name	Domestication status	Accession identifier	Accession country	Seed donor
Barley	Poaceae	*Hordeum spontaneum* K.Koch	Wild	BGE025385	Morocco	CRF
				PI 662181	Turkey	NPGS
				BGE025389	Morocco	CRF
		Hordeum vulgare L.	Landrace	BGE011162	Morocco	CRF
				BGE024314	Greece	CRF
			Improved	N.A.	N.A.	Battle*
				BGE000214	Spain	CRF
Oat	Poaceae	*Avena sterilis* L.	Wild	BGE049076	Spain	CRF
				BGE049079	Spain	CRF
				IG 100379 IFMI 3096	Turkey	ICARDA
		Avena sativa L.	Landrace	BGE008136	Spain	CRF
				BGE008166	Spain	CRF
			Improved	N.A.	N.A.	Battle*
				BGE024681	Spain	CRF
Millet	Poaceae	*Cenchrus americanus* (L.) Morrone	Wild	PI 537068	Niger	NPGS
				PEN 1028	Yemen	IPK
				PEN 1048	Yemen	IPK
			Landrace	PEN 837	Tunisia	IPK

				PEN 687	Libya	IPK
			Improved	PI 586660	Burkina Faso	NPGS
				PEN 1257	Soviet Union	IPK
Sorghum	Poaceae	*Sorghum arundinaceum* (Desv.) Stapf	Wild	PI 524718	Sudan	NPGS
				PI 482605	Zimbabwe	NPGS
				PI 539066	Soviet Union	NPGS
		Sorghum bicolor (L.) Moench	Landrace	PI 532206	Oman	NPGS
				PI 535999	Cameroon	NPGS
			Improved	PI 563327	Sudan	NPGS
				PI 563437	Chad	NPGS
Amaranthus	Amaranthaceae	*Amaranthus hybridus* L.	Wild	Ames 2072	Nepal	NPGS
				PI 500234	Zambia	NPGS
				PI 652417	Brazil	NPGS
		Amaranthus cruentus L.	Landrace	Ames 2001	Ghana	NPGS
				PI 643050	Mexico	NPGS
			Improved	AMA 169	Nepal	IPK
				Ames 15197	Argentina	NPGS
Lettuce	Asteraceae	*Lactuca serriola* L.	Wild	BGV009232	Spain	COMAV
				BGE034705	Spain	CRF
				LAC 1079	Italy	IPK
		Lactuca sativa L.	Landrace	BGV003526	Spain	COMAV
				BGV001094	Spain	COMAV
			Improved	N.A.	N.A.	Battle*
				BGV005752	Spain	COMAV
Borago	Boraginaceae	*Borago officinalis* L.	Wild	BGHZ5329	Spain	CITA
				BGHZ2103	Spain	CITA
				BGHZ4294	Spain	CITA
			Landrace	BGHZ0363	Spain	CITA
				BGHZ2340	Spain	CITA
			Improved	N.A.	N.A.	Battle*
				N.A.	N.A.	Rocalba*

Cabbage	Brassicaceae	*Brassica oleracea* L.	Wild	CGN06903	France	CGN
				CGN18947	Germany	CGN
				CGN25455	Netherlands	CGN
			Landrace	CGN14079	Belgium	CGN
				CGN15773	Portugal	CGN
			Improved	N.A.	N.A.	Rocalba*
				N.A.	N.A.	Battle*
Flax	Linaceae	*Linum usitatissimum* L.	Wild	Ames 29165	Georgia	NPGS
				PI 231945	Belgium	NPGS
				PI 253972	Irak	NPGS
			Landrace	LIN 2020	Yemen	IPK
				LIN 2288	Colombia	IPK
			Improved	BGE030455	Spain	CRF
				PI 598151	Nepal	NPGS
Okra	Malvaceae	*Abelmoschus tuberculatus* Pal & Singh	Wild	Grif 12671	India	NPGS
				PI 639676	Sri Lanka	NPGS
				PI 639681	India	NPGS
		Abelmoschus esculentus (L.) Moench	Landrace	PI 489782	Ivory Coast	NPGS
				PI 505564	Zambia	NPGS
			Improved	N.A.	N.A.	Battle*
				PI 548700	India	NPGS
Sesamum	Pedaliaceae	*Sesamum indicum* L.	Wild	SESA 17	Yemen	IPK
				SESA 20	Yemen	IPK
				SESA 22	Yemen	IPK
			Landrace	SESA 4	North Korea	IPK
				SESA 5	Irak	IPK
			Improved	N.A.	N.A.	Rocalba*
				SESA 14	N.A.	IPK
Chili pepper	Solanaceae	*Capsicum baccatum* L.	Wild	CGN21515	N.A.	CGN
				CGN16973	Bolivia	CGN
				CGN17025	Bolivia	CGN

			Landrace	CGN16972	India	CGN
				CGN23260	Bolivia	CGN
			Improved	CGN21470	Chile	CGN
				CGN22181	Peru	CGN
Tomato	Solanaceae	*Solanum pimpinellifolium* L.	Wild	BGV007948	Peru	COMAV
				LYC 1	N.A.	IPK
				LYC 2671	N.A.	IPK
		Solanum lycopersicum L.	Landrace	LYC 15	Switzerland	IPK
				LYC 1014	Guatemala	IPK
			Improved	N.A.	N.A.	Battle*
				N.A.	N.A.	Clause*
Faba bean	Fabaceae	*Vicia narbonensis* L.	Wild	IG 111590 IFVI 5266	Tunisia	ICARDA
				BGE031092	Spain	CRF
				BGE031093	Spain	CRF
		Vicia faba L.	Landrace	BGE022388	Spain	CRF
				BGE031076	Spain	CRF
			Improved	N.A.	N.A.	Rocalba*
				N.A.	N.A.	Battle*
Lens	Fabaceae	*Lens culinaris* ssp. *orientalis* (Boiss.) Ponert	Wild	PI 572374	Iran	NPGS
				PI 572399	Turkey	NPGS
				BCU001423	Turkey	BGVCU
		Lens culinaris Medik.	Landrace	PI 297287	Argentina	NPGS
				PI 298022	Turkey	NPGS
			Improved	N.A.	N.A.	Battle*
				PI 379368	Serbia	NPGS
Peanut	Fabaceae	*Arachis monticola* Krapov. & Rigoni	Wild	PI 263393	Brazil	NPGS
				PI 468196	Argentina	NPGS
				PI 497261	Argentina	NPGS
		Arachis hypogaea L.	Landrace	PI 602352	Brazil	NPGS
				Grif 373	Sudan	NPGS
			Improved	PI 538758	Burkina Faso	NPGS

				PI 550688	China	NPGS
Vetch	Fabaceae	*Lathyrus cicera* L.	Wild	BGE019570	Spain	CRF
				BGE016953	Spain	CRF
				BGE016954	Spain	CRF
		Lathyrus sativus L.	Landrace	BGE014724	Spain	CRF
				BGE046719	Spain	CRF
			Improved	LAT 440	India	IPK
				LAT 466	Soviet Union	IPK
White clover	Fabaceae	*Trifolium repens* L.	Wild	CGN22512	Uzbekistan	CGN
				CGN22513	Kyrgyzstan	CGN
				CGN22516	Kyrgyzstan	CGN
			Landrace	CGN21763	France	CGN
				CGN22506	Netherlands	CGN
			Improved	N.A.	N.A.	Intersemillas*
				CGN23145	Denmark	CGN

Table S2 Effects of evolution under cultivation on seed size, size-specific relative growth rate (sRGR), length of the vegetative growth period, initial, intermediate, and final plant sizes, yield and harvest index. All models included domestication status (Dom: 0 = wild, 1 = landrace, 2 = improved) and functional group (FG: C_3 cereals, C_4 cereals, forbs, and legumes). Species nested within accession were considered as random factors. The table shows the $F_{\text{d.f.}}$ score and significance of predictor variables (., $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). The variance of the models explained by the fixed effects is indicated by the marginal pseudo-R^2 (R^2m), and the variance explained by both the fixed and random effects is indicated by the conditional pseudo-R^2 (R^2c).

	Dom	**FG**	R^2**m**	R^2**c**
	$F_{1,107}$	$F_{3,14}$		
Seed mass	**32.1 *****	2.53 .	0.30	0.98
sRGR	1.66	**11.9 *****	0.52	0.85
sNAR	0.53	**19.0 *****	0.57	0.77
sLMR	1.08	**24.8 *****	0.76	0.99
sSLA	0.16	1.85	0.16	0.78
Growth duration	0.29	2.14	0.13	0.74
Initial size	**8.40 *****	1.43	0.18	0.94
Intermediate size	**5.41 ****	1.39	0.13	0.76
Final size	**4.18 ***	**6.70 ****	0.41	0.87
	Dom	**FG**	R^2**m**	R^2**c**
	$F_{1,62}$	$F_{3,10}$		
Yield	**4.65 ***	2.08	0.13	0.62
Harvest index	0.91	0.36	0.03	0.75

GENERAL DISCUSSION

Studying the evolution of crop traits is key to breeding crops that not only deliver improved yields, but also other ecosystem services required to ensure food security and cropland sustainability (Milla, 2023). Crop traits have changed substantially during domestication and subsequent plant breeding (Meyer & Purugganan, 2013). It is therefore important to investigate their evolution under cultivation and to find out how crops differ from wild plants. Our understanding of crop evolution comes largely from archaeology and genetics, but a trait-based ecological approach has been less well applied to address key questions for agronomical science (Garnier & Navas, 2012; Milla *et al.*, 2015). Plant size is an ecologically important trait intrinsically linked to vital rates, resource-use strategies, biotic interactions, and ecosystem processes. However, how plant size and size-related traits have evolved in crops using a trait-based ecological approach and univariate and multivariate analyses has not yet been studied in detail (Milla & Matesanz, 2017). A better understanding of this evolution requires the careful design of experiments at intra- and interspecific levels that disentangle the causes and consequences of all stages of crop evolution (selection of wild progenitors, domestication, and improvement), and delve into the mechanisms underlying phenotypic variation. In addition, the compilation of published data in global databases is needed to better generalise the results. Based on published data and new experiments, this thesis investigated in detail how several traits of crops' wild progenitors differ from those of other wild species, and whether and how domestication and improvement have changed plant size and related traits in crops. We observed that traits related to fast- or slow-growth habits have not been changed during and after crop domestication, indicating that the fast-growth habit of crops was already present in their wild progenitors (Chapter 1). We also found that selection have not led to new trait combinations, but to lower phenotypic diversity in crops compared to wild plants (Chapter 1). In Chapter 2, we linked the diverse plant growth responses to crop domestication to specific crop types, crop antiquity, geographic origin, and phylogenetic position. We found that the evolution of growth rates through domestication differs across crop types (*i.e.* grain, leaf and fruit crops), and is affected by climate and evolutionary history (Chapter 2). Other interesting findings were that the importance of the physiological, allocative and morphological components of growth differs depending on the plant organ under selection, and that domestication have changed the growth

components in opposite directions based on the crop type (Chapter 2). The final chapter asked how crops are larger than their wild progenitors, given that domestication has not consistently increased growth rates. Analysis of a comparative growth experiment with different crop species led to the finding that crop plants are larger not because of higher growth rates, but rather because they are larger-seeded (Chapter 3). Furthermore, we found that a longer growth period also plays an important role in promoting larger plants and high yields, but has not evolved consistently during evolution under cultivation (Chapter 3). In what follows, we discuss the main results, highlighting advances in the field of comparative trait-based ecology and crop domestication. We also outline implications for future breeding programmes and origins of agriculture, and recommend future lines of research that would further advance our understanding of crop evolution.

The ecological strategies of crops' wild progenitors

To understand crop evolution, we need to study not only the processes and selection pressures acting on plants during their domestication as crops, but also those acting on their wild progenitors, *i.e.* the gene pool from which domesticated populations derived. We largely ignore which plant traits distinguish wild species that were domesticated (progenitors) from those that were not, and what their ecological profiles are (Milla, 2023) The few studies that have analysed phenotypical and ecological differences between crops' progenitors and other wild species have focused mainly on competitive and reproductive traits (*e.g.* plant height, yield, seed mass, seedling size), and/or have investigated a limited range of progenitor and wild species (Cunniff *et al.*, 2014; Preece *et al.*, 2015, 2017a; Milla *et al.*, 2018), but see (Martín-Robles *et al.*, 2018) for root traits). In my thesis, we wondered whether crops' progenitors have faster resource-acquisitive traits than other wild species, by compiling leaf ecophysiological data from global databases. These comparative analyses were restricted exclusively to annual species, which include the progenitors of most major food crops, controlled for phylogeny and photosynthetic pathway (C_3 vs C_4), and distinguished between plants grown in the field and under controlled conditions. We found that crops' wild progenitors have higher photosynthetic rates, stomatal conductances, leaf nitrogen, softer leaves, and lower water use efficiency (*i.e.* higher $\delta^{13}C$) than other wild herbs that never became domesticated. These results have implications for current debates concerning the origins of agriculture and research on the ecological strategies of wild progenitors.

It has been suggested that early human selection may have favoured traits that were advantageous in the nutrient-rich and moist habitats surrounding human settlements (the so-called 'dump heap hypothesis' (Engelbrecht, 1916)). Human-induced habitat changes included woodland clearance for construction, grazing or habitation purposes, which created more open habitats (allowing higher light incidence), as well as the accumulation of domestic debris and the deposition of faeces, which improved soil nutrient content (Byrd, 2005). Early Neolithic groups tended to settle in locations with a high-water table, such as those near marshes, on lake shores, on alluvial fans, and on riverbanks (Sherratt, 1980; Kuijt & Goring-Morris, 2002). In support of this hypothesis, crops' wild progenitors would be either ruderal or competitive plants characterised by relatively rapid growth and high resource uptake rates (Grime, 1979). Some studies have shown that crops' progenitors germinate earlier, grow faster and have more acquisitive traits compared to other wild species (Cunniff *et al.*, 2014; Martín-Robles *et al.*, 2018), but the results are diverse in terms of reproductive allocation and phenology, *i.e*. traits that distinguish ruderal from competitive plants (Cunniff *et al.*, 2014; Preece *et al.*, 2015, 2017a). Although our study places crops' wild progenitors on the fast end of the leaf economics spectrum (Wright *et al.*, 2004), further studies encompassing a wider range of phenotypic traits at different levels of organization would be needed to establish whether wild progenitors are predominantly ruderals or competitors.

The acquisitive physiology of crops' wild progenitors may also be a consequence of choosing more palatable or nutrient-rich plants. Plant defence theory predicts a trade-off between growth and defence investment. Defence strategies depend on complex structural traits (such as spinescence, sclerophylly and pubescence) and chemical composition (secondary metabolites, leaf carbon nitrogen ratios), some of which are also related to leaf economics spectrum traits (Hanley *et al.*, 2007). Since both structural and chemical defences are physiologically costly and rely on the retention of resources in plant's organs, plants may face an allocation choice: 'to grow or defend' (Mattson & Herms, 1992). Investment in defence often trades-off with ecophysiological traits promoting growth and yield (Zangerl *et al.*, 1997; Bekaert *et al.*, 2012), although many factors may obscure this relationship, such as plant ontogeny or trait multi-functionality (Moles *et al.*, 2013; Barton & Boege, 2017). In addition, food quality is associated with higher nitrogen and water contents in plant tissues and lower levels of non-digestible compounds (Fernandez *et al.*, 2021; Chapuis *et al.*, 2023). By choosing more palatable or

nutrient-rich plants, early farmers could therefore have indirectly selected for plants with more acquisitive ecophysiology. Indeed, wild species of genera with crops' wild progenitors have been found to have lower levels of secondary compounds than genera without them (Garibaldi *et al.*, 2021). However, further experimental evidence looking at plant defence and nutritional quality traits is needed to test this hypothesis.

Evolution of individual plant traits under cultivation

The study of classical domestication traits, such as variations in ploidy level, loss of shattering, and increase in crop yields, has received much more attention than plant resource-use and competitive traits (Milla, 2023). Some of these ecological traits seem to react consistently to evolution under cultivation, such as plant size, seed mass and leaf area, but these findings remain to be investigated more extensively and for other size-related traits (Milla *et al.*, 2014; Kluyver *et al.*, 2017; Milla & Matesanz, 2017; Prieto *et al.*, 2017). However, traits related to resource-use, such as plant growth rates and leaf gas exchange rates, appear to respond idiosyncratically to domestication, but evidence is sparse, not comparable, and has only been evaluated in a few crop species and types (Gifford & Evans, 1981; Preece *et al.*, 2017b; Simpson *et al.*, 2017; Matesanz & Milla, 2018). In this thesis, the comparative phenotyping of wild progenitors, landraces and improved cultivars of 19 phylogenetically diverse crops allowed us to take a step forward in unveiling the differential role of domestication and later improvement in the evolution to more competitive plants.

We found that domestication, but not subsequent modern breeding, has modestly promoted large plants with large leaves and seeds. For most species, larger **plant size** is associated with higher individual reproductive output (Aarssen & Jordan, 2001) and the ability to compete in resource-rich habitats such as agricultural lands (Grime, 1974, 1979), which could explain their general increase after domestication. However, as larger plants compete more with each other (Violle *et al.*, 2009) and overinvest in support tissue at the expense of productive organs (Poorter *et al.*, 2012; Milla & Matesanz, 2017), smaller and less competitive plants can also improve the performance of crop stands (Anten & Vermeulen, 2016). Indeed, selection for communal traits such as shortened stems contributed to yield increases after the Green Revolution in some cereals (Jennings & de Jesus, 1968; Weiner *et al.*, 2010). The lack of consistent effects of modern breeding

on plant size could therefore be explained by selection for semi-dwarf varieties in some crops during recent improvement.

Plant size influences many aspects of physiology, morphology and stoichiometry (Elser *et al.*, 2010). We therefore studied leaf economics traits such as gas exchange rates, nitrogen content, specific leaf area (SLA, the ratio of leaf area to dry mass), and isotopic C composition ($\delta^{13}C$). Fast-growing plants thrive in resource-rich environments and their leaves have rapid rates of resource acquisition, low construction costs and high transpiration rates (Reich, 2014). These traits drive productivity and therefore would seem adaptive in agricultural fields. However, our results showed that none of the **ecophysiological traits** have changed in a consistent way across crops, neither during domestication nor during subsequent plant breeding. This pattern might have the following explanations:

- **Limiting factors to photosynthetic capacity**. There are limiting factors to an ever-increasing rate of resource acquisition by leaves. In angiosperms in general and in herbaceous crops in particular, photosynthesis is already maximised (Nadal & Flexas, 2018) and limited in a very well-balanced way by three limitations: stomatal, mesophyll conductance, and photochemistry (Gago *et al.*, 2019). Scaling the complexity of the three limiting factors has proven difficult and could constrain the evolution of photosynthetic capacity in crops (Flexas & Carriquí, 2020). This hypothesis is supported by the fact that crops have not increased photosynthetic rates after domestication, despite a more even distribution of stomata between both leaf sides (*i.e.* improved conductance (Milla et al., 2013)), probably due to trade-offs with the other co-limiting factors (*e.g.* reduced water use efficiency) (Flexas *et al.*, 2016). Therefore, selection for acquisitive ecophysiological traits may be compromised by the complex regulation between the factors limiting photosynthetic capacity.
- **Scaling relationships.** We found that crops tend to have larger leaves than their wild progenitors, in line with the results of other studies (Milla & Matesanz, 2017; Roucou *et al.*, 2017). An increase in leaf size is associated with higher construction and maintenance costs per unit leaf area, at the expense of a lower investment in photosynthetic machinery (Niklas *et al.*, 2007). Thus, there is a general set of scaling relationships that negatively affect the physiological functions of leaves, because increasing surface area yields 'diminishing returns' to the photosynthetic machinery.

In addition, larger leaves and plants require more supporting tissues such as petioles and stems (Poorter *et al.*, 2012). Therefore, scaling relationships cause plants to increasingly invest in stems when size increases, diverting resources from source organs.

If the rates of resource acquisition by leaves have not responded consistently to domestication, **plant growth rates** might also be unaffected. There has been much uncertainty in the literature about how relative growth rate (RGR, gains in biomass per unit biomass per unit time) has been altered through domestication. This uncertainty largely stems from the different spatial and temporal scales of analysis, diverse methods and criteria used to measure and standardise growth, as well as the different experimental conditions, which usually vary from study to study and make it difficult to generalise the results and identify the causes and limits to growth variation (Pommerening & Muszta, 2016; Hilty *et al.*, 2021). To address this issue, we (i) designed two experiments in which plants were grown under common conditions, (ii) measured their plant size non-destructively during the whole growth period, and (iii) calculated RGR and its components, using non-linear allometric growth models and a size-standardised approach. We found that RGR and its components have change in idiosyncratic ways after domestication, in line with the reactions of leaf ecophysiological traits. This seems puzzling at first instance, but several explanations might explain this pattern:

- **Trade-offs with other agriculturally relevant traits**, such as seed size. Plants with large seeds display low RGRs (Shipley & Peters, 1990; Maranon & Grubb, 1993; Swanborough & Westoby, 1996). Indeed, we found that even when RGRs are measured at similar plant sizes, this trade-off remains (but see (Paul-Victor *et al.*, 2010; Turnbull *et al.*, 2012; Simpson *et al.*, 2021)). As domestication has generally promoted large seeds (Kluyver *et al.*, 2017), increases in growth rates could have been compromised.
- **Covariations between RGR and its components**. RGR depends not only on variation in its underlying components, but also on how they covary with each other. In this regard, we found that RGR tends to covary positively with NAR and SLA, but the covariations with LMR vary in different ways depending on the crop species. The effects of domestication on the three components of RGR have been diverse and have influenced the evolution of RGR. Thus, the diverse responses of RGR components to

domestication may cancel each other out due to their covariations, resulting in little or no net effect on RGR.

- **Metabolic scaling theory** predicts there is an allometric relationship between plant growth and size, which states that RGR scales allometrically (*i.e.* non-linearly) with plant biomass, and that the exponent of this relationship within and across species is close to 3/4 (). Therefore, changes in plant size are expected to have modest effects on growth rate, because size has non-linear effects on physiology (a scaling exponent < 1). A recent study has found that the scaling exponent of growth-plant size relationships in crops is similar to that in wild species and has not changed during evolution under cultivation (Westgeest, unpubl. results). This suggests that the evolution of growth rates in crops is constrained by similar allometric relationships as in wild species, which may have prevented further evolution of growth rates.

Plant size also correlates with other traits related to plant reproduction, including **seed mass** and the time required to reach the reproductive stage ((Moles & Leishman, 2008), and references therein). Seed enlargement is one of the classic traits associated with domestication (Meyer & Purugganan, 2013), and has been observed in a wide range of crops, from cereals and legumes harvested for their seeds, to vegetables harvested for their edible leaves, stems or roots (Kluyver *et al.*, 2017). In this thesis, we also observed that crops from diverse botanical families produce heavier seeds than their wild progenitors, but this increase occurred only in early domestication and not in later improvements. There are a variety of hypotheses about the selective forces underlying seed enlargement in crops: unconscious, conscious and natural selections. For example, large seeds are thought to have been selected for their higher yields, competitive advantage, higher tolerance to deeper burial in cultivated fields, correlation with other traits such as loss of seed dormancy or higher ploidy, or through reproductive isolation in the wild (Otto & Whitton, 2000; Dempewolf *et al.*, 2012; Kluyver *et al.*, 2013; Wu *et al.*, 2019; Garibaldi *et al.*, 2021; Spengler, 2022). Exploring the selective forces that have led to heavier seeds could help to identify selection constraints and understand the causes of the emergence of the first domesticates.

Phenology is also an important component of plant size. In herbaceous plants, it is involved in the time-size trade-off, which states that earlier reproduction implies fewer resources for plant size and reproductive output, but longer development time for larger

seeds (Bolmgren & Cowan, 2008). However, phenological traits and their evolution under cultivation have received little attention in crop research (Blackman, 2017). Here, we examined how **duration of vegetative growth** changed during and after domestication, and we found that crops responded in different ways. Phenology is crucial for the adaptation of plants to their local environment in terms of daylength, temperature, precipitation, and irradiance (Chuine, 2010). Higher altitudes required adjustments mainly to the longer days of northern summers, but also to extreme cold and low irradiance. Southern tropical areas, on the other hand, required adaptations to high temperatures, as well as to greater fluctuations in water availability in the Mediterranean region (Evans, 1993). The existence of different 'centres of origin' of crops and their subsequent spread to new environments during crop diversification could lead to diverse phenological adaptations that explain the idiosyncratic responses of phenology to domestication and improvement.

Evolution under cultivation is context dependent

Once it is known how several crop traits have changed during evolution under cultivation, it is time to find out what contributes to the idiosyncratic responses of crops to domestication. Crop diversity has been well characterised recently (Meyer *et al.*, 2012; Hufford *et al.*, 2019; Milla, 2020; Milla & Osborne, 2021). For a number of crops we have evidence of when they were first cultivated, the identity, geographical distribution and environments of their wild progenitors, and the organ harvested for primary use (Milla, 2020). However, it is not clear how these crop particularities influence the evolution of crop traits. This requires experiments under common conditions involving a wide range of crop species with different origins and domestication histories, as well as multiple accessions within each domestication status. In this thesis, we found that the evolution of growth rates through domestication differs across functional groups (*i.e.* cereals, forbs and legumes), and is affected by organ under selection, climate and evolutionary history.

In northern latitudes, C_3 plants tend to grow faster because the growing season is shorter (Reich & Oleksyn, 2004). Our results showed that the effect-size of domestication (*i.e.* Hedges' *G* between landraces and progenitors) tends to be negative when wild progenitors of crops come from northern latitudes, while the domestication effect is positive when they come from southern regions. We observed the opposite trend for C_4

crops, probably because C_4 photosynthesis facilitates adaptation to different environmental conditions (Christin & Osborne, 2014), but we had very few species and it was difficult to draw conclusions. Moreover, we observed that domestication effects on the morphological component of growth (*i.e.* specific leaf area) are phylogenetically constrained, suggesting that phylogeny can partially explain the diversity of growth responses to domestication.

Finally, we found that the differential effects of domestication on sRGR components can also be explained by the organ under selection. Specifically, fruit crops have increased the physiological component of growth (net assimilation rate) during domestication, while leaf and seed crops have increased the allocative and morphological components (*i.e.* leaf mass ratio and specific leaf area, respectively). Investment in fleshy fruits can be physiologically more costly than in leaves and seeds because they are typically photosynthetic sinks that require substantial amounts of carbon, nutrients and water (Coombe, 1976). As a result, yields of fruit crops are often more limited by source strength (*i.e.* photosynthesis) rather than sink capacity (Li *et al.*, 2015a), in contrast with what occurs in seed crops such as wheat, maize and soybean (Borrás *et al.*, 2004). Overall, these results highlight that growth evolution is directly limited by environmental conditions and the balance between sink and source activities (Hilty *et al.*, 2021), and influenced by phylogeny and photosynthetic pathway (Buckley *et al.*, 2010). Understanding these constraints will inform us on the basic mechanisms of growth control and thereby improve our capacity to explain apparently idiosyncratic growth responses to domestication.

Drivers of plant size and evolution of trait–size relationships under cultivation

How can it be that crops are larger than their wild progenitors if domestication has not consistently changed leaf economics traits, growth rates and phenology? Presumably, seed mass appears to be the main underlying driver of the increase in crop size. Indeed, there is a trend for heavy seeds to produce large species (Thompson & Rabinowitz, 1989; Rees & Venable, 2007). However, the mechanism behind this positive relationship remains rather uncertain: ‘To understand the evolution of plant size, we need to consider the entire plant life cycle […], as initial size differences can persist through to maturity’ (Venable & Rees, 2009). The problem, then, is to understand how plant traits (seed mass, growth rate and lifespan) influence the evolution of plant size throughout ontogeny, while

accounting for growth differences between different sized individuals. To address this problem, we used non-linear allometric growth modelling to standardise growth at a common size between individuals, coupled with structural equation modelling to account for ontogenetic cascades.

We found that seed mass and duration of vegetative growth are the drivers with the highest influence on plant size at maturity, accounting for three-quarters of the variance in mature plant size. Thus, mature plants are larger if their seeds are heavier and they grow for longer vegetative growth spans. Although many studies have observed positive relationships between plant and seed size (e.g. (Falster & Westoby, 2005; Moles & Leishman, 2008; Du & Qi, 2010)), we provided a better mechanistic understanding for the ontogenetic coordination of mature size and seed mass. Westoby (1998) postulated that specific leaf area (a proxy for plant growth), plant height (a proxy for plant size) and seed mass can be used as independent axes of plant functioning (namely the 'LHS scheme'). Later, Díaz *et al.* (2016) proposed that two main axes –plant resource economics and the size of plants and plant organs– reflect global patterns of plant form and function. Our results appear to contradict the lack of association between plant height and seed mass, but not with growth, and support the size axis of the global spectrum of plant form and function, providing an integrated view of the role of seed size in determining plant size at different ontogenetic stages.

Regarding plant domestication, we found that the large seeds of crops have triggered the increase in mature plant size during domestication. The competitive advantage of large seeds for seedling establishment (Lush & Wien, 1980; Kidson & Westoby, 2000) and their influence on reproductive output by scaling with mature plant size (Venable, 1992) may be some of the reasons why early-domesticates were large-seeded. Another important finding was that we hardly observed any change in trait–size relationships during and after domestication. Whether crop evolution has changed trait–trait relationships is largely unknown, despite the fact that strong and complex trait relationships are a constraint to crop improvement (Milla, 2023). The evolutionary implications of seed size at different phases of plants' life cycle, the complex down-regulation of plant physiology, and the fine tuning of phenology with environmental events, as well as the close linkage of all traits to vital rates (growth, survival and

reproduction; (Moles *et al.*, 2005; Aarssen *et al.*, 2006)) may explain the high degree of coordination or phenotypic integration between the traits studied.

Consequences of having large plant size

The pattern of larger plant size can have relevant consequences for crop performance. Indeed, we found that the same traits that determine plant size at maturity (*i.e.* seed mass and duration of vegetative growth) are also the most important traits for reproductive output. In addition to plant size, we also found that reproductive output has increased over the course of evolution under cultivation. Higher individual plant yield is one of the most common characteristics that distinguish crops from their wild progenitors (Harlan et al., 1973; Meyer & Purugganan, 2013; Preece et al., 2017). We thus expected the increased yield to be a product of large plant size. However, the size-related traits studied (*i.e.* seed mass, growth rate and lifespan) hardly explain the yield increases in our set of annual herbaceous crops. Therefore, other correlated traits, not explored in this thesis, should contribute to the differences in reproductive output between domesticated plants and their wild progenitors, such as root traits and microbiome (Ehdaie *et al.*, 2010; Hamonts *et al.*, 2018; Preece & Peñuelas, 2020), changes in biomass allocation patterns such as decreased in proportion of chaff (Preece *et al.*, 2017b), genome and cell size (Roddy *et al.*, 2020), and trait inheritance and heterosis (Bruce, 1910; Williams, 1959; Fu *et al.*, 2015). Further studies are needed to determine how these other traits may underlie yield increases during crop evolution.

Curiously, our results showed that the larger size and higher yields of domesticated plants do not result in high allocation to reproductive output (*i.e.* harvest index). During modern crop breeding programmes, there has been a focus on increasing harvest index (Hay, 1995), but this can be achieved in several ways and is largely dependent on several factors such as sowing density (Qin *et al.*, 2013). Breeders are usually interested in response per unit area, not in response per individual plant. Selection for higher harvest index is often accompanied by selection for higher plant size, as plant size scales positively with reproductive output and changes in this allometric relationship may have occurred during crop evolution (Weiner, 2004; Weiner *et al.*, 2009). However, in moderate-high density stands, breeding for low-competitive phenotypes (or semi-dwarf varieties) have also increased biomass allocation to reproduction (Donald, 1951; Hay, 1995; Li *et al.*, 2015b). Indeed, the allometric relationship between plant size and density

has been used to determine the optimal plant density of crops that maximizes yield, using allometric models (Deng *et al.*, 2012a,b). Our results apply to plants grown individually, but suggest that breeders have mainly achieved increases in harvest index by improved responses to planting density.

Although the increase in plant size during crop evolution cannot be attributed to faster physiology, the selective forces acting during early choices, domestication and improvement may have had consequences on ecophysiological traits. For this reason, we compared the size and shift of phenotypic spaces of crops with respect to those of wild species, based on their ecophysiological traits. We found that early selection and/or evolution under cultivation have not led to new/unique trait combinations, but to reduced physiological diversity in crops compared to wild plants. This is in line with previous studies reporting that crops do not shift beyond the phenotypic boundaries observed in the wild (Donovan *et al.*, 2014; Rotundo & Cipriotti, 2017; Milla *et al.*, 2018; Garibaldi *et al.*, 2021), but have less variable phenotypic spaces (Lin *et al.*, 2011). However, we found the same trend here even after comparing the crop- and wild-phenotypic spaces at equal sample sizes, thus controlling for the effect of species richness. We suggest that the constrained phenotypic spaces of crops and the considerable overlap with wild spaces may be a consequence of phenotypic canalization due to inheritance from their wild progenitors, which already harboured reduced phenotypic variance in their ecophysiological traits, and the constraints of breeding for faster growth and high photosynthetic rates.

Future research lines

In light of the research presented in this thesis, it is possible to make the following recommendations for additional research that would further advance our understanding of the process of early selection and later evolution under cultivation.

- This thesis focussed on traits related to leaf ecophysiology and whole-plant growth, but data on root traits (including root exudates and root microbiome), leaf anatomical traits, biomass allocation patterns, and genome and cell size could also be acquired. A direct comparison of these traits with the vegetative and reproductive traits considered in this thesis could shed light on why the domesticated plants are higher-yielding than their wild progenitors.

- This thesis has placed crops' wild progenitors crops' on the fast-slow leaf economics spectrum. Further studies encompassing a broader range of phenotypic traits at different levels of organization would be required to establish whether wild progenitors are predominantly ruderals or competitors. To test these ideas, growth experiments comparing the responses of crops' wild progenitors and other wild species to different levels of fertility, stress, and disturbance could be conducted.
- This thesis focused on individual plants but experiments (either in field plots or under controlled greenhouse conditions) with different plant densities and domestication statuses could help understand how competitive ability has changed during plant domestication and how the response to plant density affects size/yield–trait relationships.
- The cross-species comparative analyses and the phenotypic space approach used in this thesis could also be applied to gain greater insights into the evolution of intraspecific variation in crops. The study of trait spaces within species and the processes that shaped them should also be further explored to understand the evolutionary potential of different types of traits.

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GENERAL CONCLUSIONS

- Crops and their wild progenitors share similar resource-use traits, all having higher leaf nitrogen, photosynthesis, conductance, transpiration, and softer leaves than wild species that were never domesticated. However, these traits have not consistently changed during and after domestication. Other attributes related to competitive ability (such as plant size and seed mass) do differ between domesticated and progenitor plants, suggesting that the ability to outcompete other species (through larger size) has been a more important factor in agricultural selection than resource acquisition and growth.
- Domestication began with acquisitive, and physiologically less diverse species, *i.e.* crops´ wild progenitors, which may have prevented further improvements in crop ecophysiology. Constraints on further evolution may be due to the lower phenotypic diversity, trade-offs between plant traits at different organizational levels, and limiting factors of photosynthetic capacity. Thus, the initial choice of wild species by proto farmers affects crop evolution.
- The acquisitive physiology of crops' wild progenitors could reflect their pre-adaptation to early anthropogenic water- and nutrient-rich environments and/or be an indirect consequence of the selection of palatable and nutritious wild species.
- Crops do not have unique ecophysiological traits that distinguished them from wild species – instead, their wild progenitors occupy the acquisitive end of the trait space and ecophysiological traits have not consistently changed after domestication.
- RGR is mainly driven by the physiological component and has not increased consistently after domestication, in line with reactions of leaf ecophysiolofical traits.
- The reactions of the three components of RGR –physiology, allocation and morphology– to domestication are diverse, and can cancel each other out when combined into a whole-plant level process such as RGR.
- Among crops, the responses of RGR and its components to domestication depend on environmental factors (such as climate in the geographical origin of crops) and phylogenetic position, and change markedly with the plant organ under selection.

- ❖ Wild progenitors and/or landraces harbour a greater diversity in growth traits than modern cultivars. Therefore, intraspecific diversity within species in growth traits has decreased during crop evolution.
- ❖ Plants with large seeds display low RGRs, even when RGRs are measured at similar plant sizes. Further increases in RGRs may not improve crop yields because of trade-offs with other relevant traits (*e.g.* seed size and or investment in defence).
- ❖ Growth rate is less important than seed size and duration of vegetative growth in explaining variation in mature plant size, supporting the plant size–seed size axis of variation, but also highlighting the role of phenology as a key driver of plant size.
- ❖ Ontogeny matters: The strong positive relationship between seed mass and plant size at the seedling stage implies that plants with larger initial sizes will later develop into larger mature plants, despite their lower RGRs.
- ❖ Seed mass and duration of growth is more important than RGR for increasing crop yield and could be one of the reasons why large-seeded genotypes have been selected during domestication. The high yields of modern crops are also explained by other traits not considered in this thesis, which claims for exploring other drivers of variation in crop yields.
- ❖ Seed mass and growth dynamics are highly functionally coordinated with plant size, despite shifts in trait means during crop evolution, probably due to their high joint contribution to vital rates (*i.e.* growth, survival and reproduction).