

## RESEARCH ARTICLE

# How seeds and growth dynamics influence plant size and yield: Integrating trait relationships into ontogeny

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## Abstract

1. Seeds, growth rates and duration of growth influence plant development. However, we lack a mechanistic understanding of how they lead to larger and higher-yielding plants, as these traits have not yet been explicitly studied in combination and across ontogeny. Seed size and growth dynamics have evolved differently during domestication and improvement. Nevertheless, it remains unclear whether the relationships between these traits and their contribution to plant size and yield have also changed over the course of crop evolution.
2. Here we grew wild, landrace and improved accessions of 18 annual herbaceous crops in a glasshouse. For each plant, we measured seed mass, growth rate and duration of vegetative growth. We also measured plant size at three ontogenetic stages: seedling, juvenile and mature, and reproductive output. Using path analyses, we tested causal relationships between the traits and quantified their relative importance in determining mature plant size and yield.
3. Seed mass and duration of vegetative growth were more important than growth rates in explaining variations in mature plant size and yield among species. Domesticated plants were larger, had heavier seeds and higher yields, but did not grow faster or for longer time-spans than their wild progenitors. Trait relationships did not differ between the wild, landrace and improved accessions.
4. Our results suggest that annual herbs reach larger sizes primarily through a combination of heavier seeds and longer vegetative growth periods. Moreover, domestication has increased plant size only through the heavy-seed causal pathway, via cascading effects during ontogeny. However, the high yields of modern crops hardly be explained by the traits considered here, suggesting the importance of other drivers, such as roots and their microbiome.
5. *Synthesis.* We provide a better mechanistic understanding of the size axis of global plant trait variation and emphasise the role of growth duration in explaining the diversity of mature plant sizes. Seeds and growth dynamics are highly functionally coordinated with plant size, and this coordination has changed little during crop evolution. Our results highlight that multi-trait relationships

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throughout plant ontogeny play a key role in governing how domestication has influenced plant size and crop yields.

#### KEYWORDS

crop wild progenitor, domestication and improvement, harvest index, path analysis, relative growth rate, seed size, total plant biomass, trade-offs

## 1 | 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; Kunstler et al., 2016; Niklas et al., 2003), contributing to differences in ecological strategies (Grime, 2001; Westoby, 1998). Plant size is also critical for vital rates, as it determines seedling survival, flowering and maturation times, and reproductive output (Moles & Leishman, 2008; Westerland & 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 regimes, growth form and phylogeny determine plant size (Goldberg et al., 2017; McCarthy et al., 2007; Moles et al., 2009). 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 mature plant size. Plants differ widely in their ability to acquire and allocate biomass from seedling to juvenile to mature stages (Dayrell et al., 2018; Henn & Damschen, 2021; Poorter et al., 2012). This is partly because the roles of different morphological, physiological and phenological (M-P-P) 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 interaction between different traits during plant development drives variation in mature plant size.

During ontogeny, at least three types of M-P-P traits can explain variation in mature plant size: seed size, growth rate and duration of vegetative growth (Violle et al., 2007). Seed mass influences the size of other plant organs via cascading effects during ontogeny (Roach & Wulff, 1987). For example, heavier seeds often germinate earlier in the season 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, heavier roots, and thus to larger mature plants overall (Niklas, 2004). Indeed, previous studies have found positive relationships between seed mass and seedling size at both intra- and interspecific levels

(Fenner, 1983; Jakobsson & Eriksson, 2000; Lush & Wien, 1980), as well as a positive scaling between organ sizes and whole plant size (Price et al., 2007, 2014; West et al., 1999). Also, in global analyses of functional traits, plant size and seed mass co-vary on 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 mature plants.

In addition to initial size, growth rates also contribute to variation in mature plant size. High rates of biomass gain produce increasingly larger plants. 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). RGR can 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). Thus, plants can achieve high RGRs by enhancing photosynthetic rates and/or investing more in photosynthetically active tissues (Poorter & Remkes, 1990). The interplay between the underlying components of RGR can also drive differences in mature plant size (Sun & Frelich, 2011). Finally, body size also depends on the time devoted to vegetative growth. By increasing the extent of growth, species with even smaller seeds and slow growth rates can produce larger mature plants. For example, herbs of the genus *Petasites* have the largest leaves in the British flora and a relatively long growth period compared to other herbs, yet their seeds are very small and their growth slow (Grime et al., 1988; Hodgson et al., 2017; TRY database, Kattge et al., 2020, request no. 8910, accessed 13 March 2020). Indeed, theoretical models to fit and explain plant size distributions often assume that delayed reproduction is associated with larger plant size (Cohen, 1976; Kozłowski, 1992). Moreover, previous case studies report that annual herbs that flower later tend to be larger (Bolmgren & Cowan, 2008; Sun & Frelich, 2011). Thus, the duration of vegetative growth also contributes to the variation in mature plant size.

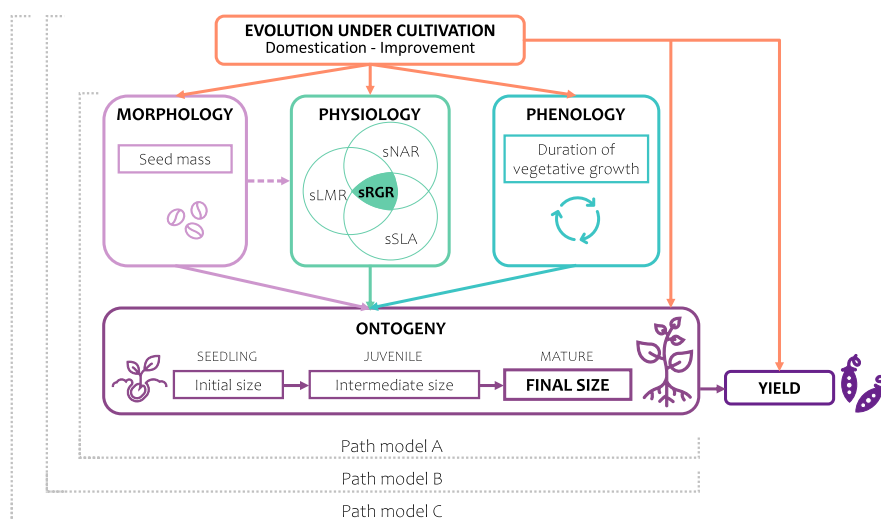
To understand the relative roles of initial size, growth rate and duration of vegetative growth in shaping mature plant size, we need to consider plant ontogeny and multiple trait correlations. Plant ontogeny comprises different developmental stages such as seedling, juvenile and mature stages (Gatsuk et al., 1980). However, the size of a mature plant has often been explained without considering ontogenetic cascades, that is, variations in the size and shape of different organs or of the whole plant due to shifts in trait-size relationships during plant development (McNamara, 2012). This approach is only appropriate if the trait-size relationships are linear or do not change

throughout plant ontogeny, but this is usually not the case. For example, seed mass has a stronger influence on seedling size than on mature plant size (Stanton, 1984). The relationship between RGR and size also shifts as plants develop (Larocque & Marshall, 1993). In addition, numerous studies have examined the trade-offs between seed mass and growth (e.g. Gleeson & Tilman, 1994; Maranon & Grubb, 1993; Poorter & Rose, 2005; Shipley & Peters, 1990; Swanborough & Westoby, 1996), but few have considered ontogeny when assessing these relationships (Cornelissen, 1999; Niinemets, 2006). Because correlations observed at the seedling stage may differ from those observed at maturity (Laughlin et al., 2017; Mason et al., 2013), understanding the causes of variation in mature 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). In addition, other changes have 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 (Gómez-Fernández et al., 2022; Harlan et al., 1973; Meyer & Purugganan, 2013). So far, however, such changes have not been linked directly or indirectly to the increases in plant size. Moreover, domestication and further improvement have differentially affected these traits, as there have been different selection pressures, human behaviours and rates of evolutionary change during these two stages of crop evolution (Abbo et al., 2014; Meyer & Purugganan, 2013). Selection for desirable characteristics over undesirable or neutral ones may have disrupted the pattern of trait-trait relationships (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 and crop yields, as well as on trait-trait relationships, are still poorly understood.

Here, we aimed to disentangle the roles of seed size, growth rate and duration of vegetative growth as drivers of mature plant size and yield in annual herbaceous crops. Instead of examining each trait individually, we asked how these drivers interact to determine mature plant size and yield through direct and indirect effects throughout ontogeny (Figure 1). We chose 18 phylogenetically diverse crops, including wild, landrace and improved accessions of each crop, because this study system provides huge variation in the ontogenetic drivers of size, and in plant size itself. Additionally, this study system allowed us to investigate the evolution of size and its drivers after plant domestication and improvement, and how that evolution impacted on crop yields. Plants were grown under common environmental conditions and assessed for size at three developmental stages: seedling, juvenile and mature. We expected that seed, growth dynamics and ontogenetic changes in plant size all interact to determine mature plant size and yield, and that domestication and improvement have exerted differential effects on plant traits and their interactions. In particular, we asked (1) what is the relative importance of seed mass, RGR and duration of vegetative growth to account for variation in mature plant size? And through which of the three RGR components do the effects of RGR mainly arise?; (2) have domestication and improvement differentially impacted mature plant size through changes in M-P-P traits and their interactions?; and (3) to what extent do crop yields depend on mature plant size and its drivers?



**FIGURE 1** A priori conceptual model for exploring the morphological, physiological and phenological traits that explain variations in plant size and yield. Seed mass, growth rate and duration of growth are interrelated and together determine plant size during ontogeny (Path model A). Evolution under cultivation, which comprises initial domestication and further improvement, affect mature plant size (Path model B) and yield (Path model C) directly or through changes in the plant traits. Ontogeny is the development of plants at different stages (seedling, juvenile and mature). Growth rate is the size-standardised relative growth rate (sRGR) and its underlying components (i.e. size-standardised net assimilation rate (sNAR), size-standardised leaf mass ratio (sLMR) and size-standardised specific leaf area (sSLA)). Solid lines indicate hypothesised positive causal relationships; dashed lines indicate hypothesised negative causal relationships; arrows represent the direction of causality.

## 2 | MATERIALS AND METHODS

We grew wild, landrace and improved accessions of 18 annual herbaceous crops under common conditions. Seed mass, RGR and its underlying components, and duration of vegetative growth were measured for a total of 378 individual plants. We also estimated the total biomass of each plant at three ontogenetic stages (seedling, juvenile and mature) and harvested its reproductive output at the fruiting stage. Using path analyses, we assessed the relative contribution of seed size, growth rate and duration of vegetative growth to plant size variation. In addition, we compared the results at different evolutionary stages by independently analysing initial domestication (wild progenitors vs. landraces) and further improvement (landraces vs. improved cultivars). Finally, for grain and fruit crops, we investigated how variation in mature plant size and its drivers impacted on crop yields.

### 2.1 | 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 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<sub>3</sub> cereals (13%), C<sub>4</sub> 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 cultivated mainly 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<sup>-1</sup> Basacote Plus 6M, Compo). 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<sup>-2</sup> s<sup>-1</sup>.

### 2.2 | 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 for 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 for plant size (see below) were measured non-destructively on the *focal plants* at regular intervals during the period of vegetative growth. We measured the same traits on 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 mass 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 the first subsection of Data analyses.

Seeds of *focal plants* were weighed individually in a Mettler Toledo MX5 microbalance (1 μg precision; Mettler Toledo). Approximately 2 weeks after sowing, three seedlings per accession from seeds of different weights (light, medium and heavy) were selected for the experiment ( $n = 126$  accessions × 3 replicates = 378 *focal plants*). Each *focal plant* was monitored individually every 3 to 8 days (8 times in total), more frequently during early growth. At each monitoring date, plant height, canopy diameter, number of tillers, number of leaves, length of longest leaf and diameter of basal stem were measured. Previous studies have shown correlations between these non-destructive traits and plant biomass (e.g. Tracey et al., 2016). In addition, the following phenological stages were recorded: germination stage (cotyledon[s] visible), early vegetative stage (first true leaves visible), late vegetative stage (several leaves and tillers), flowering stage (first flower buds visible), and fruiting stage (several open flowers/first fruit set).

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, covering all accessions ( $n = 284$  *calibration plants*). 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) and calculated the total leaf area per plant using Photoshop CS6 (Adobe Systems, Inc.). Each plant fraction was oven-dried at 60°C for 3 days and weighed. Total mass (g) per plant was calculated by adding all mass fractions at each harvest date.

### 2.3 | Data analyses

Due to its anomalous growth, one *focal plant* was excluded prior to data analysis. All analyses were performed in R v.4.2.0. (R Core Team, 2021).

**TABLE 1** Common and botanical names of the wild and domesticated taxa of each of the 18 crops included 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	<i>Hordeum spontaneum</i> K.Koch	<i>Hordeum vulgare</i> L.	C <sub>3</sub> cereal
Oat	<i>Avena sterilis</i> L.	<i>Avena sativa</i> L.	C <sub>3</sub> cereal
Pearl millet	<i>Pennisetum glaucum</i> (L.) R.Br.	<i>Pennisetum glaucum</i> (L.) R.Br.	C <sub>4</sub> cereal
Sorghum	<i>Sorghum arundinaceum</i> (Desv.) Stapf	<i>Sorghum bicolor</i> (L.) Moench	C <sub>4</sub> cereal
Amaranth	<i>Amaranthus hybridus</i> L.	<i>Amaranthus cruentus</i> L.	Forb
Lettuce	<i>Lactuca serriola</i> L.	<i>Lactuca sativa</i> L.	Forb
Borage	<i>Borago officinalis</i> L.	<i>Borago officinalis</i> L.	Forb
Cabbage	<i>Brassica oleracea</i> L.	<i>Brassica oleracea</i> L.	Forb
Flax	<i>Linum usitatissimum</i> L.	<i>Linum usitatissimum</i> L.	Forb
Okra	<i>Abelmoschus tuberculatus</i> Pal & Singh	<i>Abelmoschus esculentus</i> (L.) Moench	Forb
Sesame	<i>Sesamum indicum</i> L.	<i>Sesamum indicum</i> L.	Forb
Chilli pepper	<i>Capsicum baccatum</i> L.	<i>Capsicum baccatum</i> L.	Forb
Tomato	<i>Solanum pimpinellifolium</i> L.	<i>Solanum lycopersicum</i> L.	Forb
Faba bean	<i>Vicia narbonensis</i> L.	<i>Vicia faba</i> L.	Legume
Lentil	<i>Lens culinaris</i> ssp. <i>orientalis</i> (Boiss.) Ponert	<i>Lens culinaris</i> Medik.	Legume
Peanut	<i>Arachis monticola</i> Krapov. & Rigoni	<i>Arachis hypogaea</i> L.	Legume
Vetch	<i>Lathyrus cicera</i> L.	<i>Lathyrus sativus</i> L.	Legume
White clover	<i>Trifolium repens</i> L.	<i>Trifolium repens</i> L.	Legume

### 2.3.1 | Calibration and estimation of biomasses

Using the *calibration plant* data, we fitted linear mixed-effects models (LMMs) 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), several models were run with different combinations of non-destructive traits and time interval between sowing and harvesting dates as fixed effects. A combined variable between crop species 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 Akaike Information Criterion (AIC). The final models, which explained on average 99% of the variance in response variables, were:

$$\text{Total mass} \sim \text{height} + \text{canopy} + \text{leaf no.} \quad (1)$$

$$+ \text{leaf length} + \text{basal diameter} + \text{time}$$

$$\text{Leaf mass} \sim \text{height} + \text{canopy} + \text{leaf no.} \quad (2)$$

$$+ \text{leaf length} + \text{basal diameter} + \text{time}$$

$$\text{Leaf area} \sim \text{canopy} + \text{tiller no.} + \text{leaf no.} \quad (3)$$

$$+ \text{leaf length} + \text{basal diameter} + \text{time}$$

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 open flowers. For each *focal plant*, the minimum and maximum biomass estimated during the vegetative growth period were recorded as seedling size (or initial size) and mature size (or final size), respectively. Therefore, mature size, also referred to as final size in this study, refers to the size of a plant when it reaches sexual maturity. Juvenile size (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 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 mature stage.

### 2.3.2 | 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 of 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, for each *focal plant*, 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:

$$\text{sRGR} = \frac{(1/k)(A - \ln M_c)(B - \ln M_c)}{(A - B)}, \quad (4)$$

where *M<sub>c</sub>* 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 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 leaf mass to total plant mass at the common size) and size-standardised SLA (sSLA, the ratio of leaf area to leaf mass at the common size). sRGR can be factored into its three components as follows (Hunt, 1982):

$$\text{sRGR} = \text{sNAR} \times \text{sLMR} \times \text{sSLA}. \quad (5)$$

Thus, size-standardised NAR (sNAR) was estimated as the ratio between sRGR and the product of sLMR and sSLA.

### 2.3.3 | 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 3 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 mature plant size and yield. Since not all plants reached the fruiting stage, yield and harvest index were determined only for those plants 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.

Overall, four separate datasets were compiled. First, the *full dataset* collected data on seed mass, sRGR and its components, duration of vegetative growth, and initial, intermediate and final sizes for each *focal plant* ( $n = 377$ ). From this dataset, two separate datasets were derived: one including wild and landrace accessions (*domestication dataset*;  $n = 269$ ) and another including landrace and improved accessions (*improvement dataset*;  $n = 215$ ). Finally, we also had data on yield and harvest index for a number of *focal plants* that formed the *yield dataset*. This dataset included 201 *focal plants* belonging to 14 crop species, with each crop species comprising wild and domesticated accessions.

### 2.3.4 | Statistical analyses testing the effects of evolution under cultivation on plant traits

To evaluate the effects of evolution under cultivation on seed mass, sRGR and its components, duration of vegetative growth, plant sizes (i.e. initial, intermediate and final sizes), yield and harvest index, we ran LMMs using the *lme* function in the `nlme` R package (Pinheiro et al., 2021). Models included domestication status (categorical

variable: wild progenitor, landrace, improved cultivar) and functional group (categorical variable: C<sub>3</sub> cereal, C<sub>4</sub> cereal, forb, legume) as fixed effect factors, and accession identity nested within crop species as a random factor over the intercept. Models for yield and harvest index were based on the *yield dataset*, while the *full dataset* was used for the other response variables. 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<sup>2</sup> with the *rsquaredGLMM* function in the `MuMIn` R package (Barton, 2020). Multiple comparison tests between domestication statuses were performed using the *glht* function in the `MULTCOMP` R package and false discovery rate correction (Hothorn et al., 2008).

### 2.3.5 | Path analyses

To investigate the causal relationships between plant traits and the effects of evolution under cultivation on these relationships, we used path analysis based on previous knowledge (i.e. confirmatory path analysis sensu Shipley, 2000). Path analysis combines the results of multiple individual models jointly and allows for testing direct and indirect causal relationships between several predictor and response variables (Grace, 2006). We chose a piecewise approach to path analysis because it allows for the inclusion of random effects in the individual models (Lefcheck, 2016). All individual models that composed a path model were run using LMMs and included accession nested within crop species as random effects. We proposed three a priori path models to answer the three study questions (Figure 1; Table 2). The first model, **Path model A**, which aimed to examine the relative importance of seed size, growth rate and duration of vegetative growth in determining mature plant size, considered the following expectations:

- Seedlings from heavy seed tend to be larger than those from light seed, so they are more likely to establish and compete better for resources (Kidson & Westoby, 2000; Lush & Wien, 1980). Seed reserves generally 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, but its effects mainly occur in the early stages of plant development and gradually decrease during 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 sRGR to also explain variation in plant size.
- The organs of seedlings are generally smaller than those of mature plants and these size differences increase with the duration

**TABLE 2** Workflow of the methods showing the specific questions addressed in the study, the conceptual model implemented in the path analysis, the dataset used, and the figure and/or table showing the results for each question. The specific questions are grouped under the three general questions asked in the Introduction section

Question	Conceptual model	Dataset	Output
(1) What is the relative importance of seed size, growth rate and duration of growth to explain variations in plant size?	<p>Path model A</p>	Full dataset	Figure 3 Table S3
Through which of the three sRGR components do the effects of sRGR on plant size mainly arise?	<p>Path model A</p>	Full dataset	Figure S3
(2) Has domestication impacted mature plant size through modulation of M-P-P traits?	<p>Path model B</p>	Domestication dataset	Figure 4 Table S4
Has improvement impacted mature plant size through modulation of M-P-P traits?	<p>Path model B</p>	Improvement dataset	Figure 4 Table S5
Has evolution under cultivation differentially impacted on trait–trait relationships?	<p>Multigroup analysis</p>	Full dataset	Figure S4
(3) To what extent do crop yields depend on mature plant size and its drivers?	<p>Path model C</p>	Yield dataset	Figure 5 Table S6

Note: For trait icons see [Figure 1](#).

Abbreviations: M-P-P traits, morpho-physio-phenological traits; sRGR, size-standardised relative growth rate.

of vegetative growth (Dosio et al., 2003). Therefore, we assumed that plant size also depends on the time devoted for growth.

- A trade-off between seed mass and RGR is well established in the literature, so we specified a negative relationship between them (Gleeson & Tilman, 1994; Maranon & Grubb, 1993; Poorter & Rose, 2005; Shipley & Peters, 1990; Swanborough & Westoby, 1996; but see Paul-Victor et al., 2010; Simpson et al., 2021; Turnbull et al., 2012).
- Positive scaling relationships between organs and plant sizes are frequently reported (Falster et al., 2008; Niklas, 2004). We therefore expected seedling size to influence juvenile size

and ultimately mature plant size via cascading effects during ontogeny.

This path model was fitted to the *full dataset*. Since the drivers and effects of sRGR may be different for each of its components (i.e. sNAR, sLMR and sSLA), we also fitted this path model by replacing sRGR with its components and specifying bivariate correlations between them ([Figure 1](#); [Table 2](#)). Prior to analysis, we ln-transformed mass and growth variables to avoid non-linear relationships between them, and scaled duration of vegetative growth (mean = 0, SD = 1). Since a diversity of domestication statuses and functional groups

was considered in the selection of accessions and crop species, domestication status and functional group were included as exogenous categorical variables to control for experimental design. We hypothesised that domestication status has an impact on M-P-P traits and mature plant size, as changes in these traits during evolution under cultivation have been frequently reported (e.g. Gómez-Fernández et al., 2022; Harlan et al., 1973; Meyer & Purugganan, 2013; Milla & Matesanz, 2017). We also assumed that M-P-P traits and mature plant size depend on functional group affiliation, since species belonging to the same functional group tend to have a close evolutionary history ( $C_3$  cereals,  $C_4$  cereals and legumes are separate clades) and respond similarly to environmental conditions (Reich et al., 2003). In the presence of heteroscedasticity (evaluated with Levene's test), we used the 'varldent' weights specification within the *lme* function.

Second, to examine how initial domestication and subsequent improvement affected mature plant size through modulation of M-P-P traits, **Path model B** was fitted separately to the *domestication* and *improvement* datasets (Figure 1; Table 2). This path model tested the expectation that domestication and improvement may have differentially altered seed mass, sRGR, duration of vegetative growth, and mature plant size, as well as their relationships (Abbo et al., 2014). Individual models were specified as explained for Path model A. However, to obtain a coefficient for the path from domestication and improvement, domestication status was coded as an exogenous ordinal variable (0 = wild progenitor, 1 = landrace, 2 = improved cultivar). Alternatively, to test how the pattern of trait-trait relationships differed among wild progenitors, landraces and improved cultivars, we conducted a multigroup path analysis (Table 2). This analysis determined whether the coefficients of each path varied among domestication statuses.

Third, we investigated whether and how variations in mature plant size and its drivers affect crop yields during evolution under cultivation (Figure 1; Table 2). To this end, we fitted the **Path model C**, which was an extended version of Path model B, but with additional paths to crop yield based on the following assumptions. Yield increases with the size of mature plants, especially in annuals, which re-allocate a fraction of their vegetative biomass to reproduction at maturity (Weiner et al., 2009). Yield often decreases with duration of vegetative growth, 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). Therefore, we hypothesised that yield (i) increases with mature plant size, (ii) decreases with duration of vegetative growth and (iii) has improved during evolution under cultivation. Since several proxies for yield show phylogenetic signals (Martin, 2021), we also assumed that yield depends on functional group affiliation. This path model was fitted to the *yield* dataset (Figure S1) and the individual models were specified as explained for Path model B.

All path 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. A path model is

considered consistent when the *C* statistic is not significantly different from a  $\chi^2$  distribution ( $p > 0.05$ ). We also calculated the AIC score to know the relative support for each path model (Shipley, 2013). We standardised the coefficients to allow direct comparisons between relationships that are measured on different scales. To assess the relative importance of predictor variables on mature plant size and yield, we calculated the direct, indirect and total effects using the standardised path coefficients as follows (Shipley, 2000). 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 predictor was quantified by calculating the marginal and conditional pseudo- $R^2$ . d-sep tests, Fisher's *C*, AIC, standardised path coefficients, pseudo- $R^2$ , and multigroup analysis were performed with the *PIECEWISESEM* R package (Lefcheck, 2016).

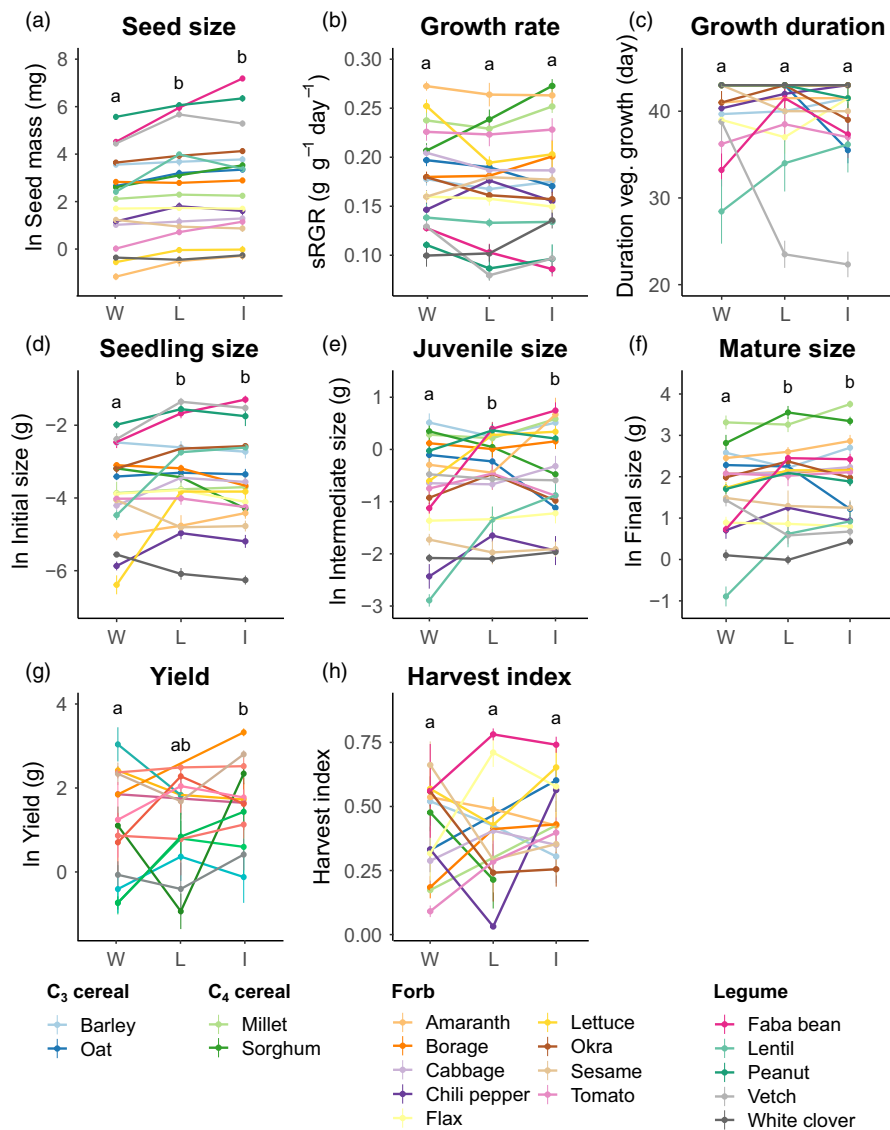
### 3 | RESULTS

There was considerable variation in the predictor variables across the 18 crops studied (Figure 2). The largest-seeded crop had seeds three orders of magnitude heavier than the smallest-seeded crop (faba bean: 548 mg vs. amaranth: 0.57 mg). This comprises ca. a quarter of the range of variation reported worldwide for this trait (Westoby et al., 1992). sRGR and duration of vegetative growth varied to a lesser extent, from 0.10 for peanut to  $0.27 \text{ g g}^{-1} \text{ day}^{-1}$  for amaranth, and 25 for tomato to 43 days for white clover, respectively. Response variables also varied greatly among crops. Mature 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; Figure 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 (Figures 3–5).

#### 3.1 | Evolution of traits under cultivation

Domesticates had heavier seeds, larger seedlings, larger juvenile and mature plants, and higher yields than their wild progenitors, regardless of their functional group (Figure 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 shown by the high proportion of variance explained by the random part of the models (Figure S2; Table S2). On the other hand, sRGR and its components, duration of vegetative growth and harvest index did not differ between domestication statuses, but did differ between





**FIGURE 2** Trait variation by domestication status (W = wild progenitor, L = landrace, I = improved cultivar). The circles are the sample mean scores, with error bars extending 1 SD from the means. Colours represent different crop species. Different letters indicate significant differences at  $p < 0.05$  after Tukey's post hoc test and false discovery rate correction. Trait abbreviations: Seed size, seed mass; sRGR, size-standardised relative growth rate; Growth duration, duration of vegetative growth; Initial size, total plant dry mass at the seedling stage; Intermediate size, total plant dry mass at the juvenile stage; Final size, total plant dry mass at the mature stage; Yield, dry mass of reproductive output for seed and fruit crops; Harvest index, the ratio of yield to the sum of final plant size and yield.

functional groups for sRGR, sNAR, and sLMR (Figure 2b,c,h; Table S2). Domestication and improvement had different effects on plant traits. In particular, domestication increased seed mass, and initial, intermediate and final sizes, while modern breeding only increased yield (Figure 2).

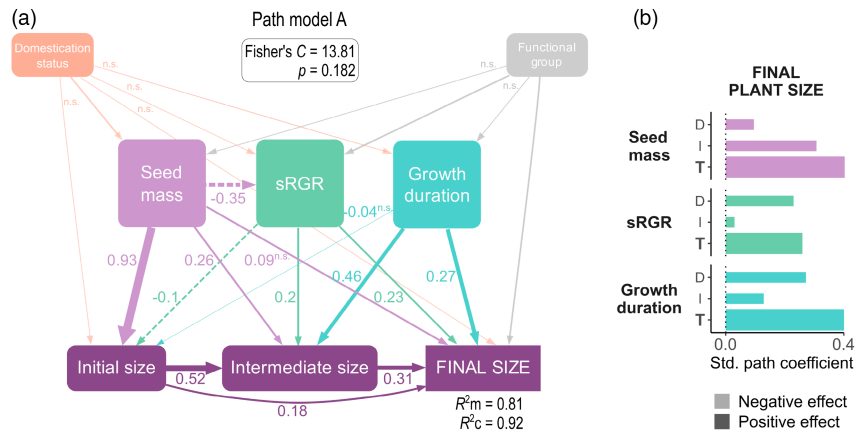
### 3.2 | Relationships among seed mass, growth rate and duration, and plant size (Path model A)

Heavier seeds grew into larger seedlings and juvenile plants, which ultimately affected mature size (Figure 3a; Table S3). Plant traits strongly interacted with each other during ontogeny. Seed mass promoted larger plants especially in the early ontogenetic stages, while growth rate and duration did so later on (Figure 3a; Table S3). Thus, large mature plants were driven directly by rapid growth and longer growing periods and indirectly by the effect of seed mass on seedling size (Figure 3b). Heavier seeds provided slower growth rates (Figure 3a; Table S3), but we found no clear causal relationships

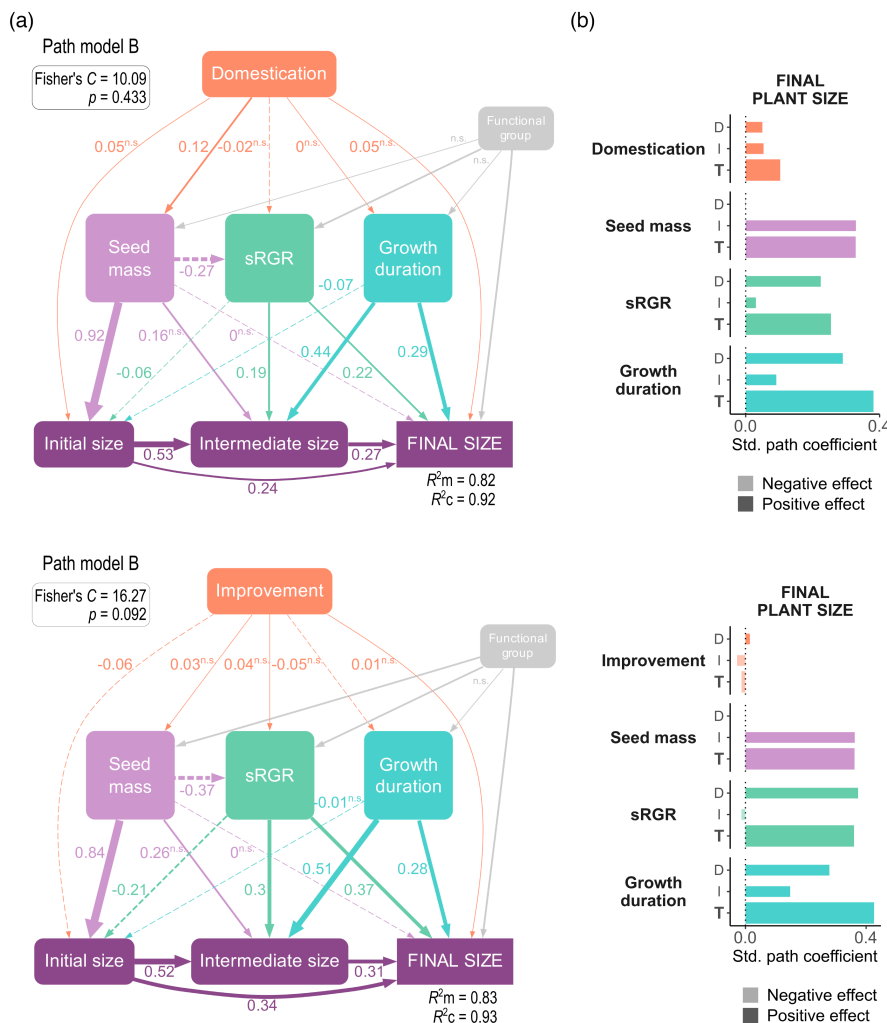
between seed mass and sRGR components (Figure S3a). sNAR was the component that accounted for most of the contribution of sRGR to final plant size (Figure S3b). Overall, seed mass and duration of vegetative growth explained most of the variation in final plant size (Figure 3b).

### 3.3 | Separate effects of domestication and improvement (Path model B and Multigroup analysis)

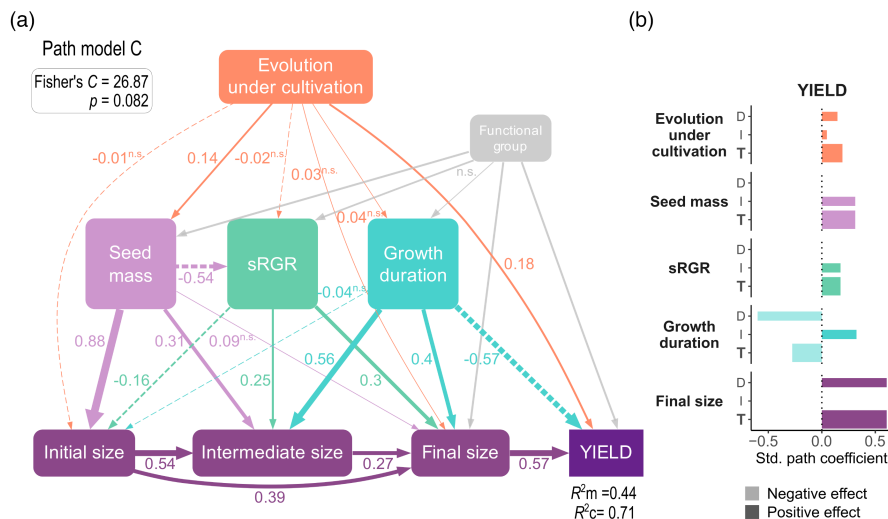
The models run separately for domestication and improvement differed from each other in the importance of the different M-P-P traits in defining final plant size, but the paths did not differ in direction and statistical significance (Figure 4; Tables S4 and S5). Domestication increased final plant size via changes in seed mass, while modern breeding slightly decreased it through negative effects on seedling size (Figure 4a; Tables S4 and S5). In both models, seed mass and duration of vegetative growth were the main drivers of final plant size, but during improvement, sRGR became more



**FIGURE 3** (a) Path model A of causal relationships between seed mass, growth rate and duration, and plant size for the *full dataset* (i.e. all plants included in the study). Domestication status and functional group were included as exogenous categorical variables (domestication status: wild progenitor, landrace, improved cultivar; functional group: C<sub>3</sub> cereal, C<sub>4</sub> cereal, forb, legume). Solid arrows (→) are positive effects and dashed arrows (→) are negative effects. Arrow widths are proportional to the magnitude of the standardised 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 ( $R^2_m$ ) and conditional ( $R^2_c$ ) pseudo- $R^2$  are the proportion of variance in final plant size explained by fixed effects and all effects (fixed plus random effects), respectively. The global model fitted the data (Fisher's C = 13.81, df = 10,  $p = 0.182$ ,  $n = 377$ ). For trait abbreviations see Figure 2. (b) Synthesis of direct, indirect and total effects of seed mass, sRGR and growth duration on final plant size, derived from (a). Direct effects (D) are the standardised 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).



**FIGURE 4** (a) Path model B of causal relationships between seed mass, growth rate and duration, and plant size, and the effect of evolution under cultivation for the *domestication* (wild progenitors vs. landraces; top) and *improvement* (landraces vs. improved cultivars; bottom) datasets. Domestication and improvement were included as exogenous ordinal variables (domestication: 0 = wild progenitor, 1 = landrace; improvement: 1 = landrace, 2 = improved cultivar) and functional group as an exogenous categorical variable (C<sub>3</sub> cereal, C<sub>4</sub> cereal, forb, legume). The meanings of path coefficients, line styles, arrow widths, and pseudo- $R^2$  are the same as in Figure 3. The global model fitted the data (for *domestication dataset*: Fisher's C = 10.09, df = 10,  $p = 0.433$ ,  $n = 269$ ; for *improvement dataset*: Fisher's C = 16.27, df = 10,  $p = 0.092$ ,  $n = 215$ ). For trait abbreviations see Figure 2. (b) Synthesis of direct, indirect and total effects of domestication/improvement, seed mass, sRGR, and growth duration on final plant size, derived from (a). The meaning of the direct (D), indirect (I) and total effects (T) is the same as in Figure 3.



**FIGURE 5** (a) Path model C of causal relationships between seed mass, growth rate and duration, plant size and yield, and the effects of evolution under cultivation for the *yield* dataset (i.e. seed and fruit crop plants that reached the fruiting stage). 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<sub>3</sub> cereal, C<sub>4</sub> cereal, forb, legume). The meanings of path coefficients, line styles, arrow widths, and pseudo- $R^2$  are the same as in Figure 3. The global model fitted the data (Fisher's C = 26.87,  $df = 18$ ,  $p = 0.082$ ,  $n = 201$ ). For trait abbreviations see Figure 2. (b) Synthesis of direct, indirect and total effects of evolution under cultivation, seed mass, sRGR, growth duration, and final plant size on yield derived from (a). Direct effects (D) are the standardised 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).

important (Figure 4b). The pattern of trait–trait relationships was very consistent among wild progenitors, landraces and improved cultivars (Figure S4). However, size-cascading effects during ontogeny and a few effects of growth rate and duration changed in magnitude among domestication statuses (Figure S4).

### 3.4 | Consequences of plant size and its drivers on crop yields (Path model C)

Evolution under cultivation increased crop yields, mainly through other factors not accounted for by our models (direct path: 0.18; Figure 5a; Table S6). Of the traits considered in this study, seed mass mediated 18.5% of the effects of evolution under cultivation on crop yields. Final plant size was the most important trait in determining yield, followed by seed mass, duration of vegetative growth and finally sRGR (Figure 5b). Large plants that grew over a shorter period of time produced higher yields (Figure 5a; Table S6). The negative effects of duration of vegetative growth on yield were buffered by its indirect effects through plant size (Figure 5a; Table S6). Seed mass and sRGR increased yield indirectly through their effects on plant size during early and late ontogeny, respectively (Figure 5a; Table S6).

## 4 | DISCUSSION

We found that final 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 duration of vegetative growth were the drivers with the highest influence on plant size at maturity, accounting for three-quarters of the variance in final size. Thus, mature plants were larger if their seeds were heavier and they grew for longer vegetative growth periods. Domesticated plants showed a modest increase in final plant size, and evolution under cultivation only increased seed size, but 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.

### 4.1 | Proximal drivers of variation in mature plant size and crop yields

Our results show that seed size, growth rate and duration of vegetative growth account for a large variance in final plant size. Thus, a small set of M-P-P traits can explain most of the variation in final plant size. Vegetative biomass has been described mathematically as a function of these M-P-P traits (Violle et al., 2007), and positive correlations between these functional traits and mature plant size have been previously reported (e.g. Du & Qi, 2010; Falster & Westoby, 2005; Herron et al., 2021; Leishman et al., 1995). However, few studies have explicitly assessed the causal structure of trait interactions driving differences in mature plant size, and even fewer

have quantified their relative importance (Milla & Matesanz, 2017; Vile et al., 2006). Moreover, these studies provided only indirect evidence, as phenological traits were not considered and proper growth experiments were not conducted. Here, we found that although increased growth rate favoured the development of large plants, its relevance was lower than that of seed mass and duration of vegetative growth. 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 plant size. Looking at the global scale, seed mass and plant size co-vary and are orthogonal to plant resource economics (Díaz et al., 2004, 2016). At this 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 growth duration as a key driver of mature plant size.

We show that the relative importance of M-P-P 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 duration of vegetative growth became more important for plant size. The fact that trait effects change during ontogeny can make it difficult to identify causal relationships between traits and the strength of interactions. For example, when seed mass is not directly correlated with mature size, this is usually 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 might be relevant to maturity via ontogenetic cascades. 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 during 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 strong modulating effect on plant traits and their interactions, and highlights the need to consider multi-trait relationships throughout 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 a large final plant size. Consistent with this, reproductive output has been found to be positively correlated with vegetative biomass in annual plants, both between and within species (Aarssen & Jordan, 2001; Chambers & Aarssen, 2009; Lutman et al., 2011; Sugiyama & Bazzaz, 2002). However, we found that plant yield was driven by the same traits that determined final plant size at maturity in our set of annual herbaceous crops. As with final plant size, seed mass and duration of vegetative growth were the most relevant traits determining plant yield. Although both traits strongly influenced reproductive output, only seed mass changed

consistently during evolution under cultivation. Duration of vegetative growth and its evolution under cultivation has received less research attention (Blackman, 2017). As it is an environmentally responsive trait, a long vegetative growth period 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.

## 4.2 | The roles of domestication and improvement in promoting larger 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 decreases during later improvement, e.g. in oat (Figure 2; Figure S5). Previous studies have also found a general increase in mature plant size after domestication, despite differences between crops (Martín-Robles et al., 2018; Milla et al., 2014; Milla & Matesanz, 2017). However, the proximal mechanisms leading to such post-domestic upsize were previously unknown. Here, we show that the larger seeds of domesticated accessions triggered a pronounced increase in plant size early in ontogeny and a more modest increase in final plant size. Physiological and phenological traits, on the other hand, did not mediate the effects of domestication on plant size, as neither duration of vegetative growth nor sRGR and its components changed consistently during evolution under cultivation, in line with previous studies (e.g. Evans, 1993; Gómez-Fernández et al., 2022; Meyer & Purugganan, 2013; Preece et al., 2017). 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 show 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 Figure 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, such as cell division and expansion (Arendt, 2007; Cheniclet et al., 2005), genome size (Roddy et al., 2020) and genetic control of organ and body sizes (Busov et al., 2008; Mizukami, 2001). Furthermore, plant size in combination with planting density directly impacts on crop yields (Preece et al., 2018; 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 *full dataset* and for the *domestication* and *improvement datasets* taken separately. In other words, the patterns of trait–trait relationships (i.e. magnitude, direction and significance of paths) were highly consistent among 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). Also, since evolution under cultivation in our study only led to consistent changes in seed mass, its effects may not have been sufficient to decouple the patterns of trait–trait relationships that existed in the 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 mature size, and to survive a longer juvenile period, species with a large mature size need to have (i) a high seedling survival rate, achieved by producing larger seeds, and later (ii) a high competitive ability, achieved by rapid growth rates (Aarssen et al., 2006; Moles et al., 2005). Therefore, we argue that the relationships between traits that are closely linked to vital rates throughout ontogeny are too robust to be easily decoupled.

## 5 | CONCLUSIONS

Previous work has identified plant traits whose variation impacts on mature plant size (e.g. Violle et al., 2007). However, their relative importance remained unexplored. Here we show that seed mass and duration of vegetative growth are the main drivers of variation in mature 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 growth duration in varying mature plant size. Furthermore, our results suggest that seed mass and growth dynamics 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 shed 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 throughout ontogeny, as well as the use of size-standardised measurements, are needed to strengthen our mechanistic understanding of the evolution of crop yields.

### AUTHOR CONTRIBUTIONS

Alicia Gómez-Fernández and Rubén Milla designed the study. Alicia Gómez-Fernández collected the data. Alicia Gómez-Fernández and Rubén Milla analysed the data. Alicia Gómez-Fernández wrote a first draft of the paper and Rubén Milla contributed to further revisions. Both authors read and approved the final version.

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### CONFLICT OF INTEREST

The authors declare no conflict of interest.


### PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13979>.

### DATA AVAILABILITY STATEMENT

The raw data and R code used for data processing are available at <https://doi.org/10.6084/m9.figshare.20398878.v1> (Gómez-Fernández & Milla, 2022).

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## SUPPORTING INFORMATION

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

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