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

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Summary

- 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.

Keywords: domestication, functional groups, leaf mass ratio, net assimilation rate, relative growth rate, specific leaf area, *Triticum turgidum* L., wild progenitors

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

106 the differences among crops in the effects of domestication on RGR could also be
107 explained by phylogenetic relationships among species, as RGR and its components
108 show phylogenetic signal (Kempel *et al.*, 2011; Atkinson *et al.*, 2016).
109 Our major crops were domesticated over the last c. 10,000 years, and modern
110 varieties are the product of the last c. 100 years of intensive breeding for high-yielding
111 crops. Here, we explore the extent to which domestication and modern plant breeding
112 have impacted RGR and its components in a wide range of herbaceous crops. We
113 conducted two experiments: an intensive one, in which the domestication history of
114 durum wheat was addressed in detail, and an extensive one, in which 18 crop species
115 were investigated more broadly. In both experiments, we grew multiple accessions of
116 wild progenitors, landraces, and improved cultivars of each crop under common
117 conditions and non-destructively measured their growth dynamics using a size-
118 standardized approach (Rees *et al.*, 2010). By comparing landraces with their wild
119 progenitors and with improved cultivars, we addressed the effects of domestication and
120 modern breeding, respectively. To investigate differences among taxa, we also collected
121 data on the origin and domestication history of each crop. Specifically, we asked: i)
122 How have domestication (wild progenitors *vs*. landraces) and modern plant breeding
123 (landraces *vs*. improved cultivars) impacted crop growth rates?; ii) Which components
124 of RGR have changed the most during crop evolution?; and iii) Can changes in growth
125 rates be explained by phylogeny, organ under selection, time in cultivation, and climate
126 at crop origin?
127
128 **Materials and Methods**
129 Two experiments were carried out to investigate how growth rates evolved after
130 domestication and modern plant breeding. The first experiment, called the *intensive*
131 *experiment*, examined in detail the variation in growth rate during the evolution of
132 durum wheat (*Triticum turgidum* L.). The second experiment, the *extensive experiment*,
133 explored growth rate changes after domestication and further improvement in a diverse
134 set of 18 crops. In both experiments, we estimated total mass, leaf mass, and leaf area at
135 different times during the vegetative growth period on individual plants. Using non-
136 linear growth models, we obtained the relative growth rate and its components at a
137 common size. Finally, we computed the magnitudes and directions of domestication and
138 improvement effects for all 19 crops and tested whether they varied as a function of the
139 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

503 progenitors have faster growth rates and lower defensive traits than other wild species
504 that have not been selected for agricultural purposes.

505 In this study, sNAR was the main driver of variation in sRGR, which is
506 consistent with previous work (Shipley, 2006; Cunniff *et al.*, 2014; Atkinson *et al.*,
507 2016; but see Lambers & Poorter, 1992 and Wilson *et al.*, 1999 for contrasting results).
508 However, the magnitude of change in sNAR during crop evolution was less than in
509 sSLA and sLMR. Previous literature suggests that selection for higher yields has not
510 altered crop physiology as much as allocation patterns and morphology (Gifford &
511 Evans, 1981; Gifford *et al.*, 1984; Richards, 2000; Driever *et al.*, 2014; Sinclair *et al.*,
512 2019). For example, traits such as high harvest index (*i.e.* the ratio of yield to
513 aboveground mass), lower allocation to chaff and pods, lower root mass fraction, or
514 larger leaves and stems are more often claimed to drive yield (Evans & Dunstone, 1970;
515 Donald & Hamblin, 1976; Sinclair, 1998; Waines & Ehdaie, 2007). In addition, other
516 traits typically associated with the domestication syndrome, such as large initial and
517 final body size, earlier reproduction, and lower branching have also contributed to
518 higher yields (Preece *et al.*, 2015; Holland *et al.*, 2019; Houshmandfar *et al.*, 2020). In
519 our study, the strong physiological basis of sRGR supports the notion that physiology
520 has not consistently changed over the course of evolution under cultivation and is
521 therefore not a major driver of variation in crop yield.

522 It is noteworthy that the changes in growth traits were greater after
523 domestication than in later plant breeding. In fact, the magnitude of domestication
524 effects was *c.* 74% greater than that of further breeding. This is consistent with other
525 studies. For example, wild progenitors and landraces of wheat and maize show higher
526 phenotypic diversity than modern cultivars for root or kernel traits (Flint-Garcia *et al.*,
527 2009; Roucou *et al.*, 2017). One explanation for these results is that the domestication
528 process, when broadly defined, *i.e.* from the initial domestication of wild progenitors to
529 their spreading and diversification into landraces, spanned longer periods of time,
530 whereas modern breeding practises began about a century ago (Faris, 2014). Moreover,
531 the current study compared landraces with wild progenitors from diverse geographical
532 regions, where natural selection pressures might be different. On the other hand, modern
533 cultivars are derived from a limited number of landraces and intensive artificial
534 selection for specific traits, which in turn has reduced phenotypic and genetic diversity
535 (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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Author Contribution

AG-F and RM designed the study. AG-F, CI, GG, and JP collected the data. AG-F, MR, and RM analysed the data. AG-F wrote a first draft of the paper, and CPO, JP, MR, and RM contributed to further revisions. All authors read and approved the final version.

Data Availability

The raw data and R codes supporting the findings of this study are available at https://doi.org/10.6084/m9.figshare.16818046.v2.

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Figure legends

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).

Supporting Information

Fig. S1 Comparison of three alternative approaches to calculating RGR.

Fig. S2 Comparison of size- and time-standardized RGR.

Fig. S3 Comparison of growth curve parameters between functional groups and domestication statuses in the *extensive experiment*.

Fig. S4 Comparison of growth curve parameters between domestication statuses in the *intensive experiment*.

Fig. S5 Pairwise correlation between sRGR and its components.

Fig. S6 Relative importance of the three components of growth on the variation of sRGR.

Fig. S7 Average sRGR as a function of mean annual temperature at crop origin.

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

Table S2 List of accessions used in the *extensive experiment*, including accession identifier, functional group, domestication status, seed donor, country of origin, and geographic coordinates of the collection site.

Table S3 List of accessions used in the *intensive experiment*, including accession identifier, domestication status, seed donor, country of origin, and geographic coordinates of the collection site.

Table S4 ANOVA results on the influence of 19 bioclimatic variables on changes in growth traits during domestication.

Table S5 ANOVA results on the influence of 19 bioclimatic variables on changes in growth traits during improvement.

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

Methods S2 Details on the calculation of growth traits.

961 **Tables**

962 **Table 1** Common and botanical names of the crop species used in the two experiments,
963 as well as their domestication status (W = wild progenitor; D = domesticate) and
964 functional group affiliations. In the *extensive experiment*, domesticate status refers to
965 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 $F_{d.f.}$ 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

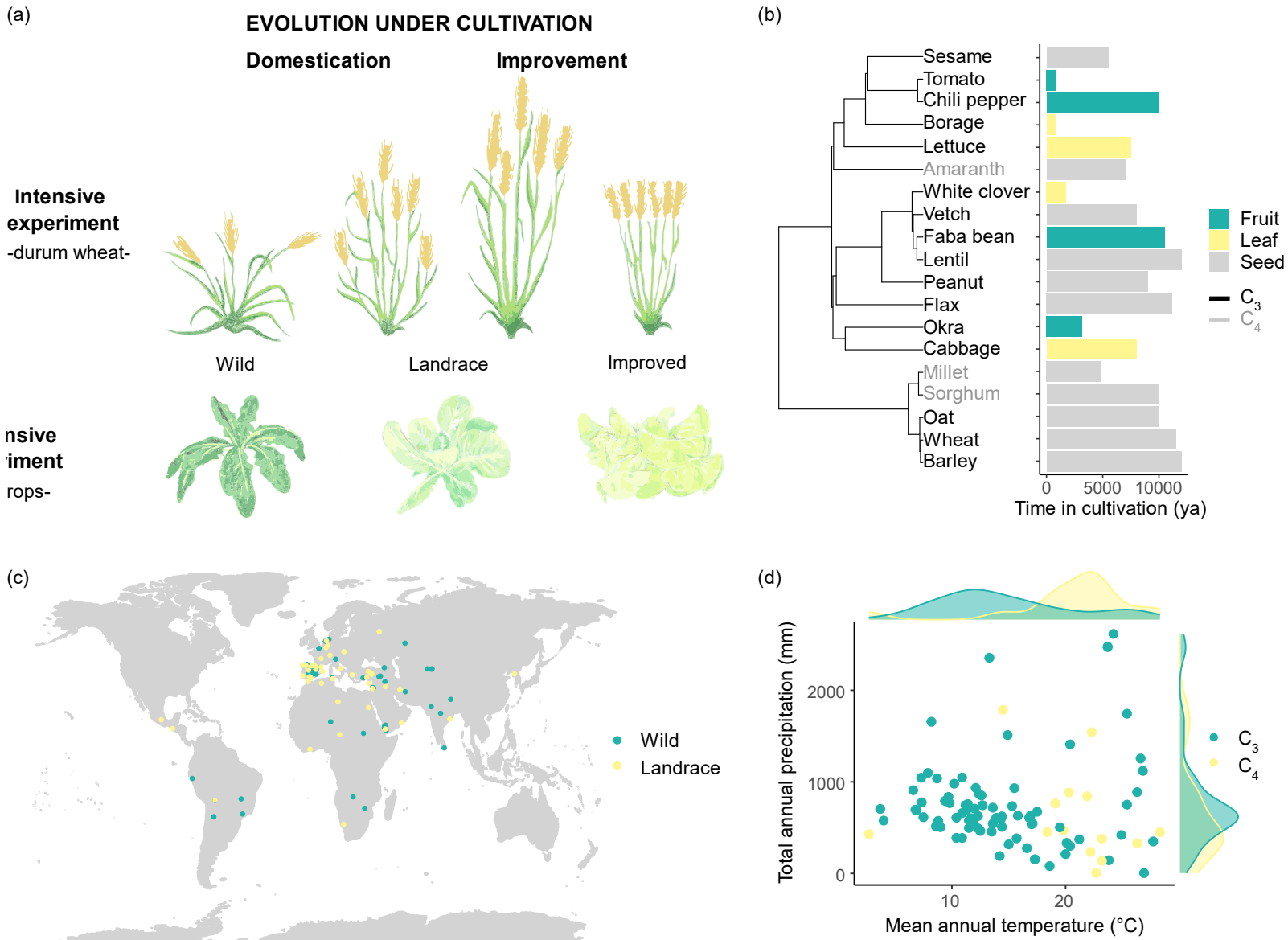
977 **Table 3** Effects of early domestication (earlyDom), late domestication (lateDom), and
978 improvement (Imp) on size-specific relative growth rate (sRGR), net assimilation rate
979 (sNAR), leaf mass ratio (sLMR), and specific leaf area (sSLA) in the *intensive*
980 *experiment*. Accession was considered as a random factor. The table shows the $F_{\text{d.f.}}$
981 score and significance of predictor variables. Significant values ($P < 0.05$) are
982 highlighted in bold. The variance of the models explained by the fixed effects is
983 indicated by the marginal pseudo-R^2 (R^2m), and the variance explained by both the fixed
984 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	***R*²m**	***R*²c**	**lateDom**	***R*²m**	***R*²c**	**Imp**	***R*²m**	***R*²c**
	$F_{1,14}$			$F_{1,14}$			$F_{1,14}$		
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

Fig. 1


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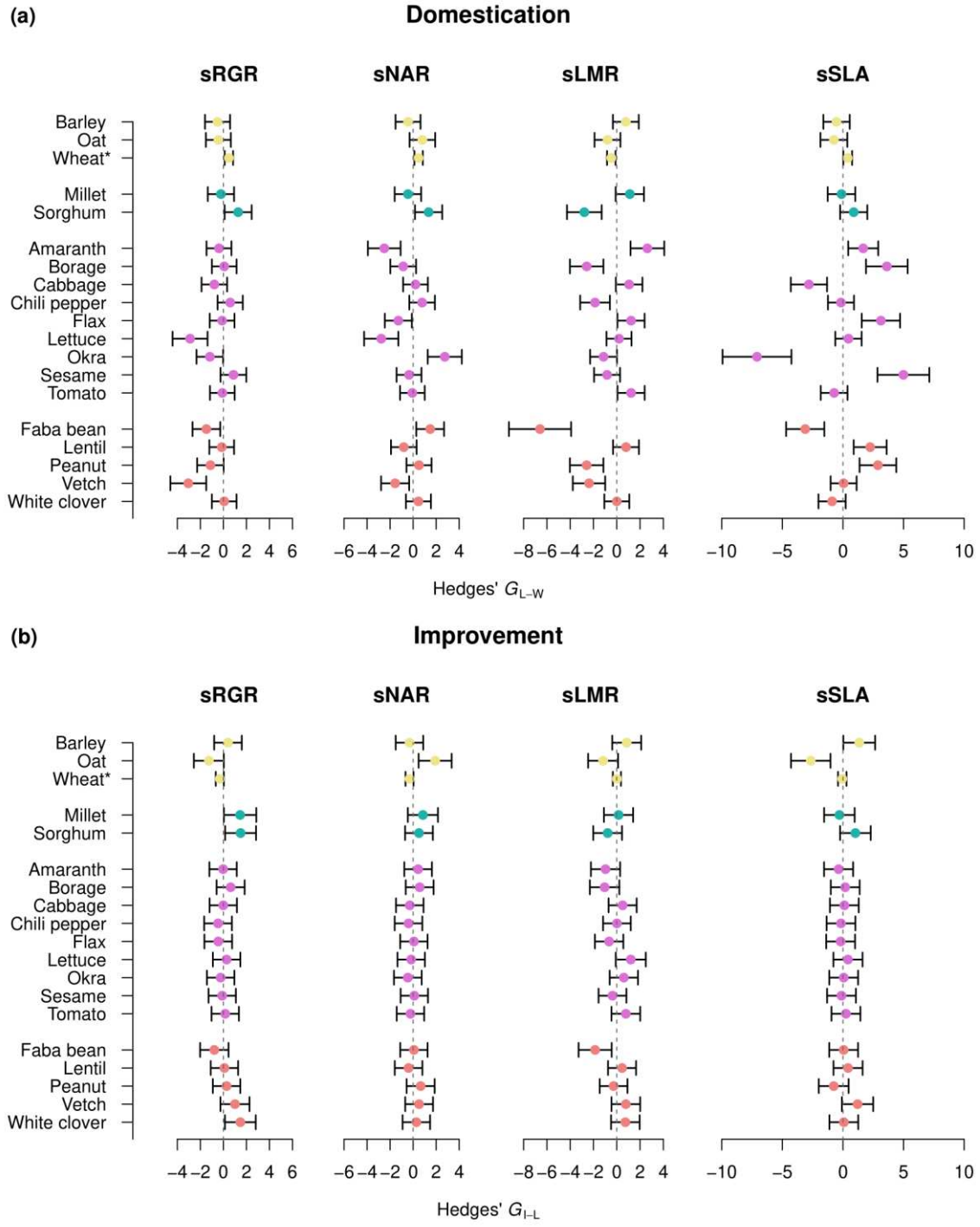
1000
0
10
20
Mean annual temperature (°C)
C3
C4

Fig.2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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
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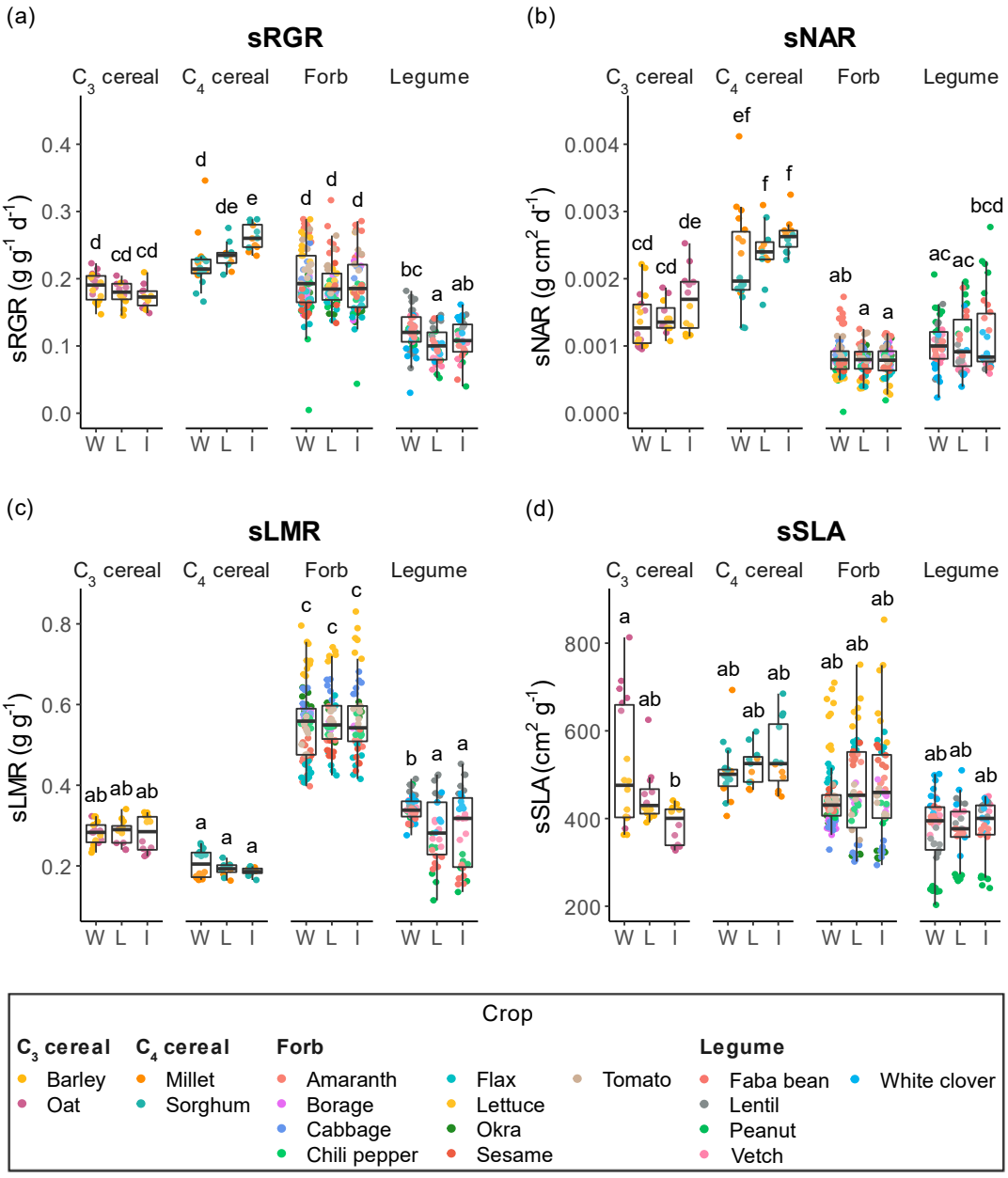
Hedges' G_{I-L}

Fig. 3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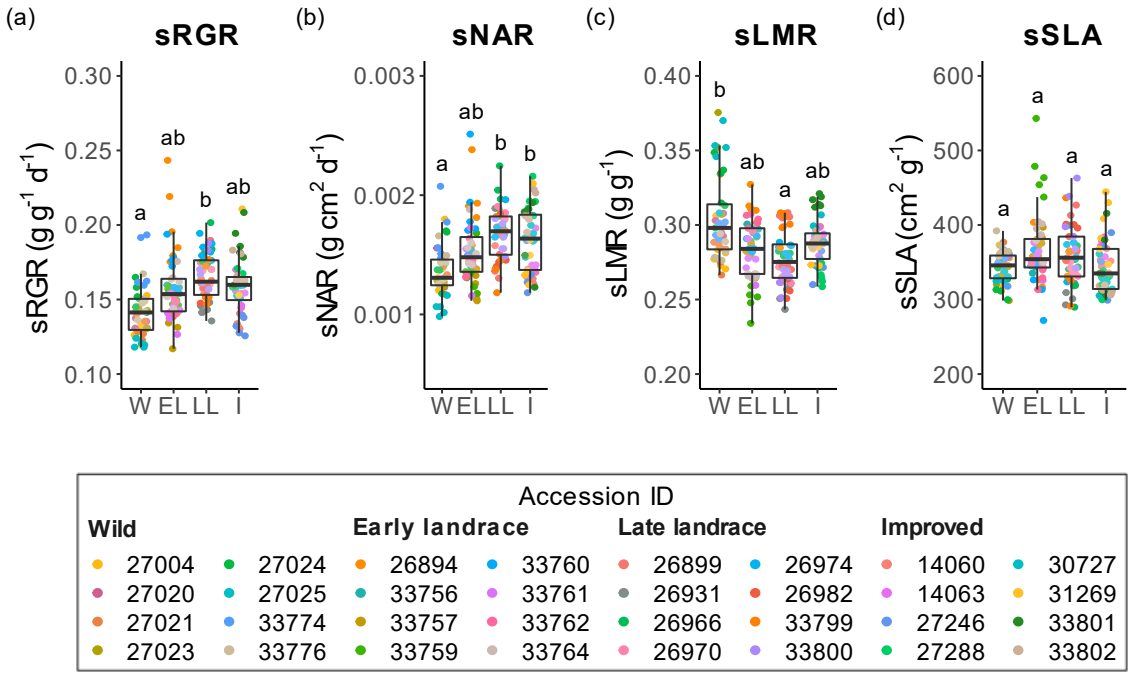
sRGR
C3 cereal
C4 cereal
Forb
Legume
sRGR (g g-1 d-1)
(b)
sNAR
sNAR (g cm2 d-1)
(c)
sLMR
sLMR (g g-1)
(d)
sSLA
sSLA (cm2 g-1)
W L I
Crop
C3 cereal
Barley
Oat
C4 cereal
Millet
Sorghum
Forb
Amaranth
Borage
Cabbage
Chili pepper
Flax
Lettuce
Okra
Sesame
Tomato
Legume
Faba bean
Lentil
Peanut
Vetch
White clover

Fig. 4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sRGR
sRGR (g g-1 d-1)
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0.25
0.20
0.15
0.10
a
ab
b
ab
W EL LL I
(b)
sNAR
sNAR (g cm-2 d-1)
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0.002
0.001
a
ab
b
b
W EL LL I
(c)
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sLMR (g g-1)
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0.35
0.30
0.25
0.20
b
ab
a
ab
W EL LL I
(d)
sSLA
sSLA (cm2 g-1)
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500
400
300
200
a
a
a
a
W EL LL I
Accession ID
Wild
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27021 33774
27023 33776
Early landrace
26894 33760
33756 33761
33757 33762
33759 33764
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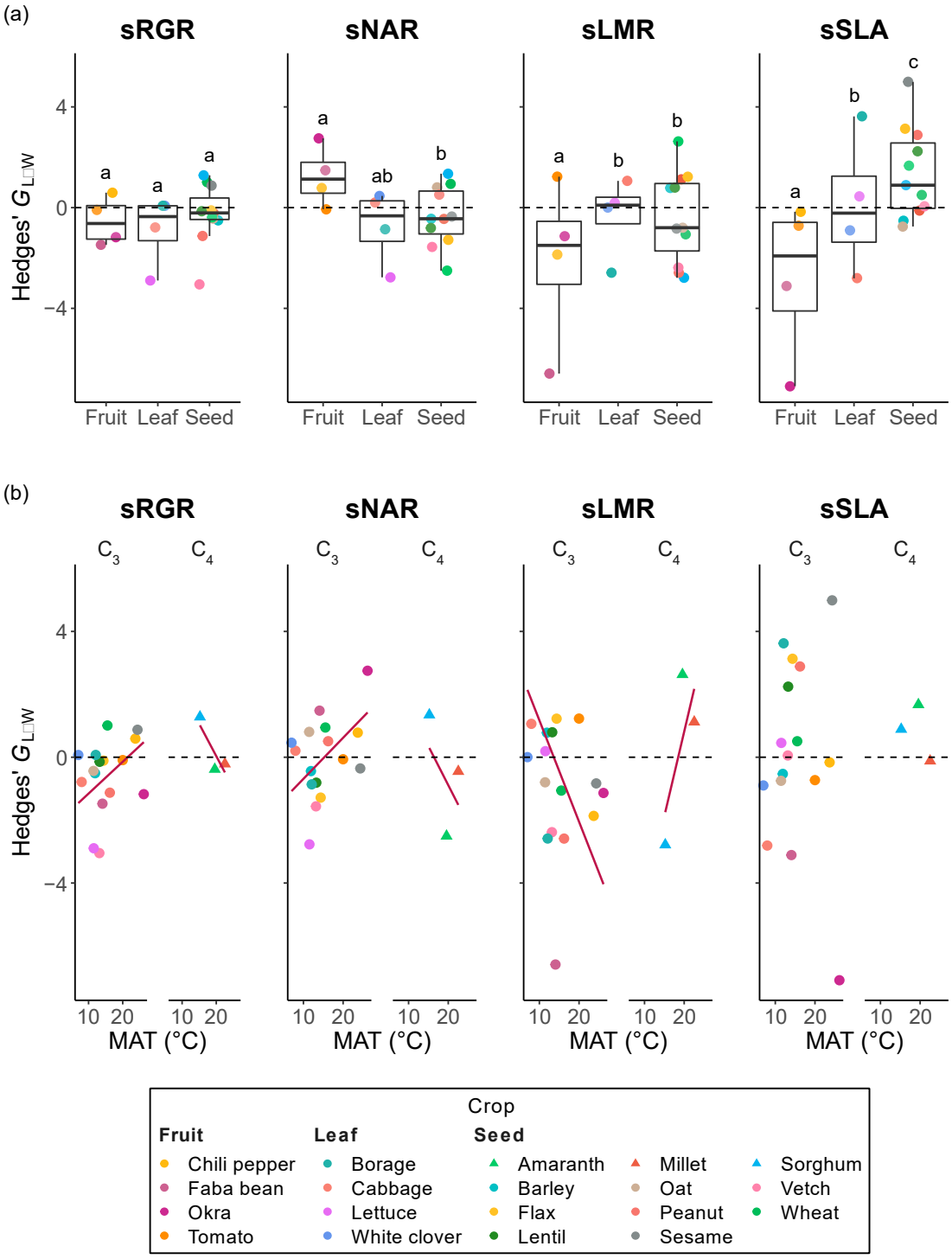
Fig. 5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sRGR
sNAR
sLMR
sSLA
Hedges' G_{LRR}
4
0
−4
a
a
a
a
ab
b
a
b
b
a
b
c
Fruit
Leaf
Seed
(b)
C_3
C_4
10
20
MAT (°C)
Crop
Fruit
Chili pepper
Faba bean
Okra
Tomato
Leaf
Borage
Cabbage
Lettuce
White clover
Seed
Amaranth
Barley
Flax
Lentil
Millet
Oat
Peanut
Sesame
Sorghum
Vetch
Wheat

New Phytologist **Supporting Information**

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

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

Article acceptance date: 24 October 2021.

The following Supporting Information is available for this article:

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Fig. S4 Comparison of growth curve parameters between domestication statuses in the *intensive experiment*.

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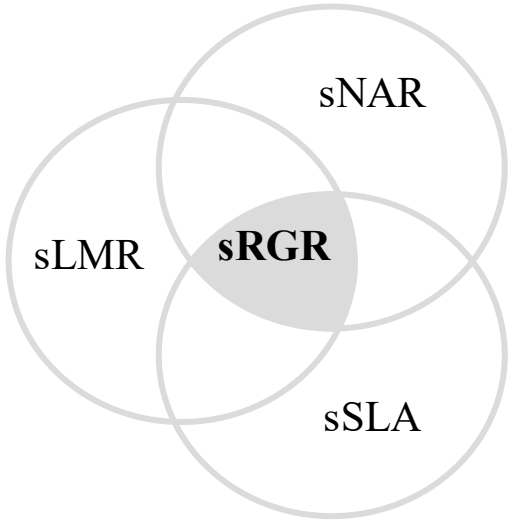
Trait	Abbr.	Definition	Formula	Unit
Size-specific relative growth rate	sRGR	The rate of dry mass accumulation at a specific plant size per unit of existing dry mass	$\frac{1}{M}\frac{dM}{dt}$	g g^{-1} d^{-1}
Size-specific net assimilation rate	sNAR	The rate of total dry mass increase at a specific plant 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.

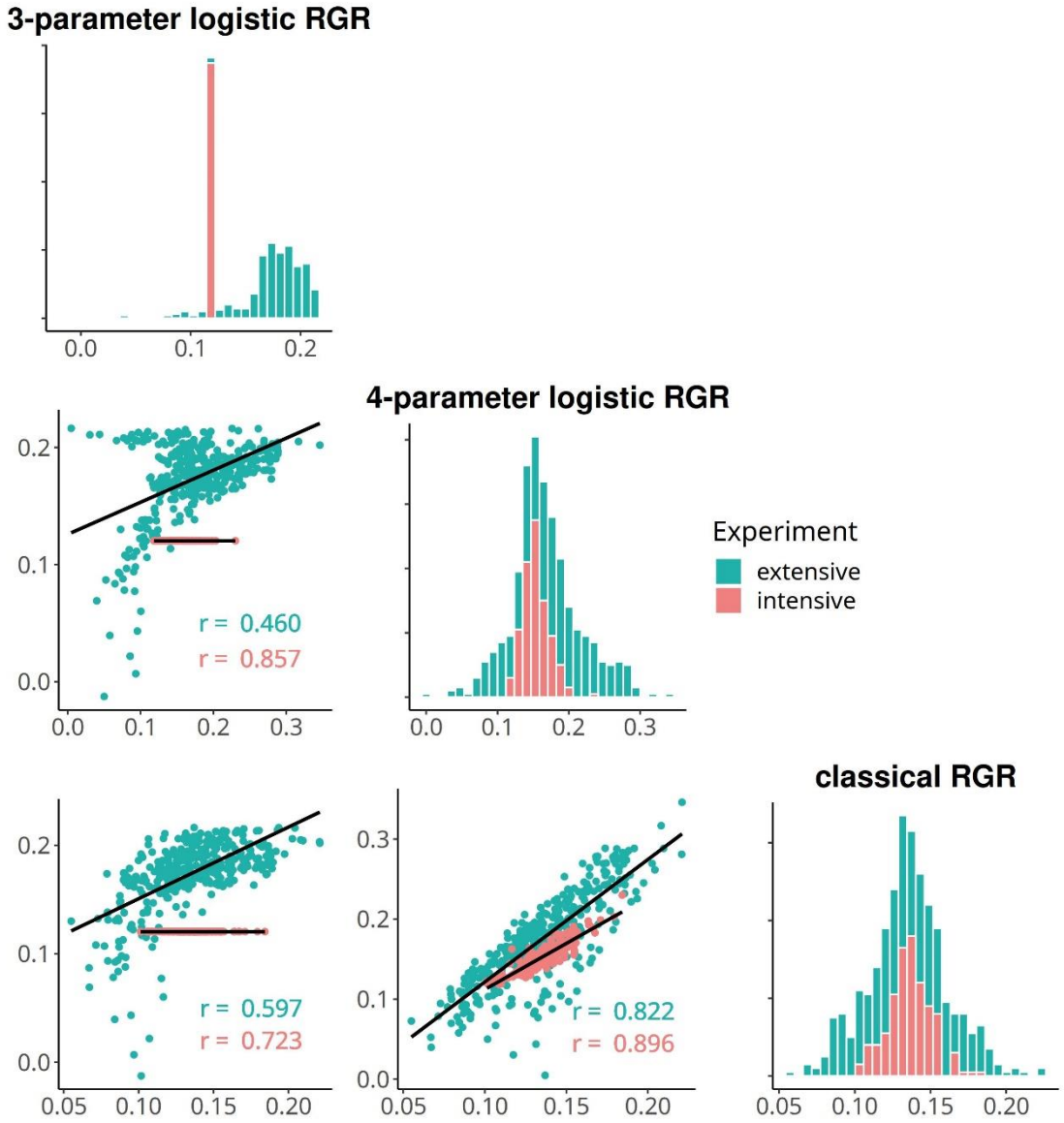
Table S4 Effects of the 19 bioclimatic variables at the geographic origin of each crop on the effect size of domestication (Hedges' $G_{L\text{-}W}$) on size-specific relative growth rate (sRGR), net assimilation rate (sNAR), leaf mass ratio (sLMR), and specific leaf area (sSLA). Models included the 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.

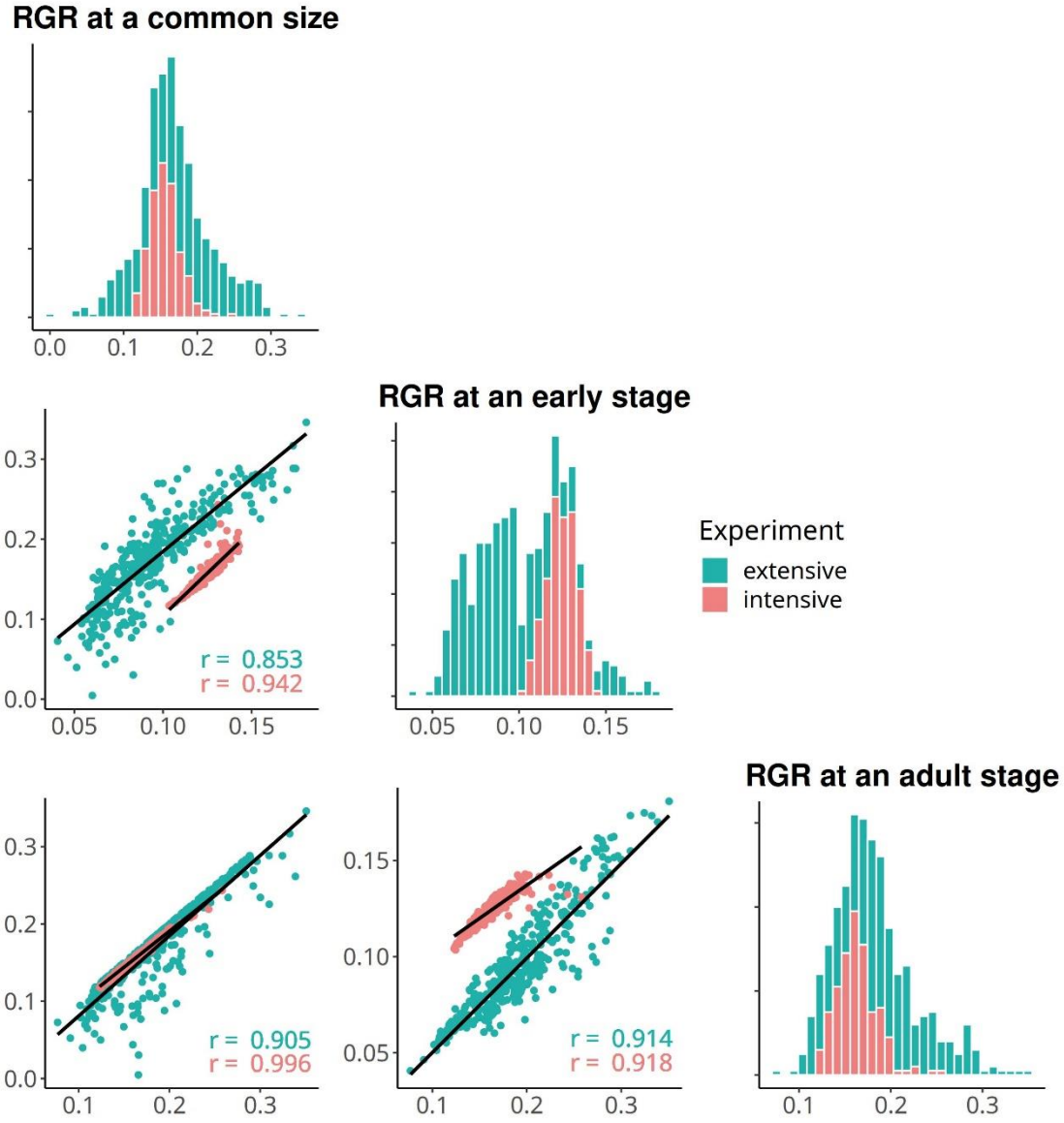


Fig. S3 Comparison of growth curve parameters in the *extensive experiment*, plotted separately by functional group: C_3 cereals, C_4 cereals, forbs and legumes, and by domestication status: wild (W), landrace (L), and improved (I) accessions. The parameters are: (a) minimum asymptote (*i.e.* the lower 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.

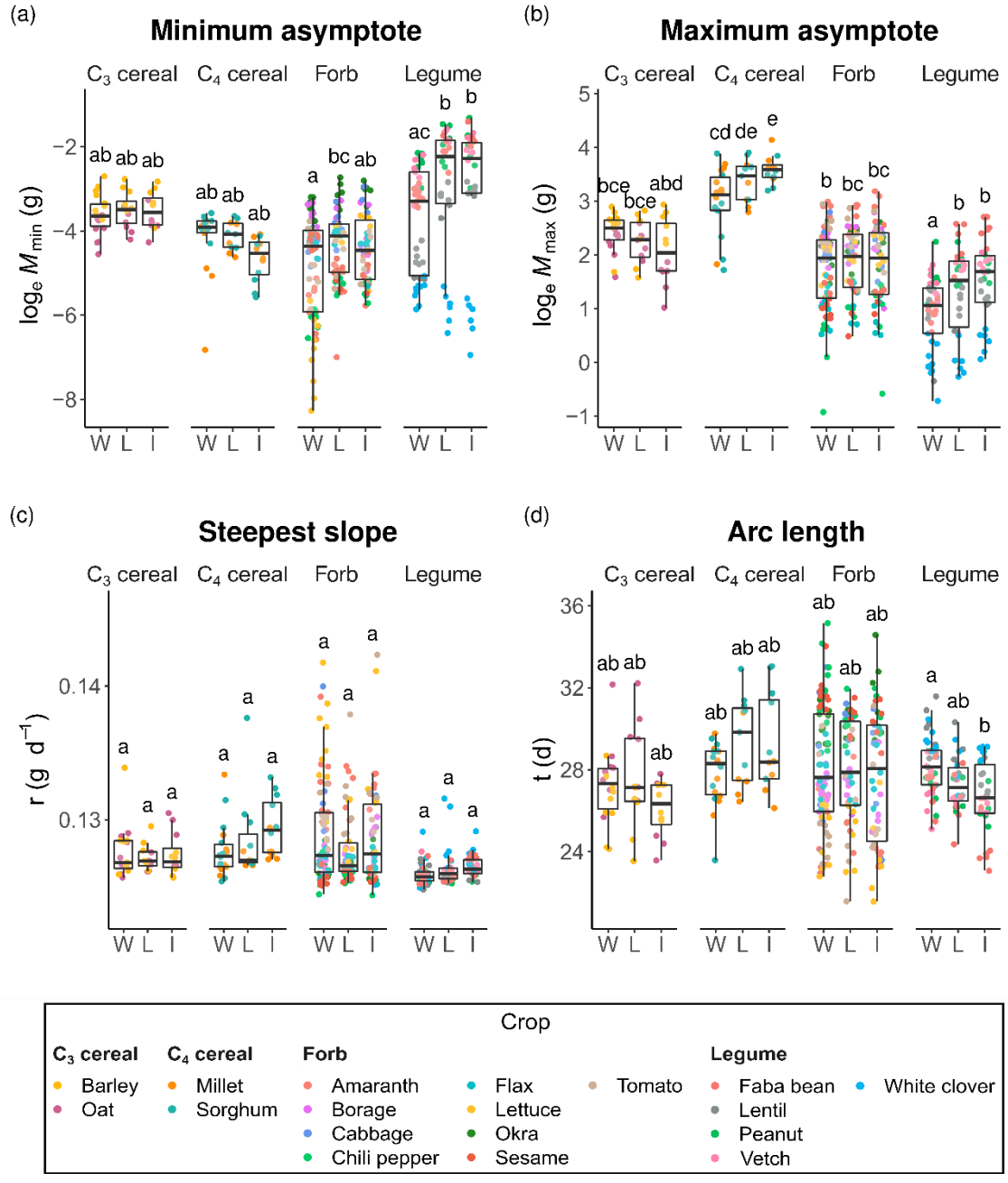


Fig. S4 Comparison of growth curve parameters in the *intensive experiment*, plotted separately by domestication status: wild (W), early landrace (EL), late landrace (LL) and improved (I) accessions. The parameters are: (a) minimum asymptote (*i.e.* the lower horizontal asymptote), (b) maximum asymptote (*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.

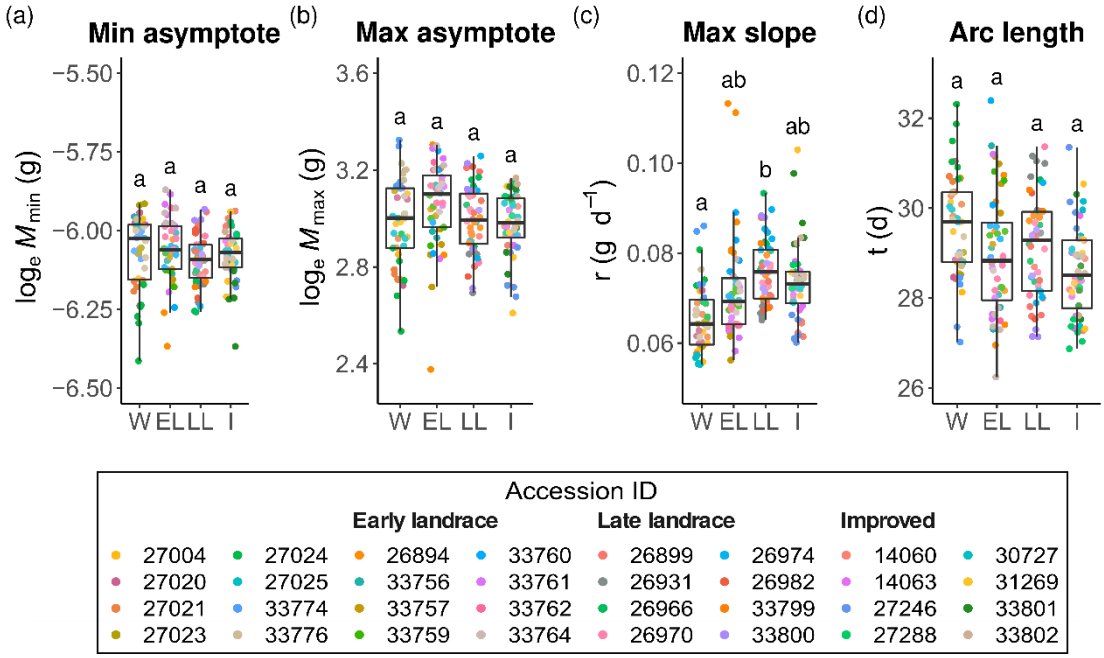
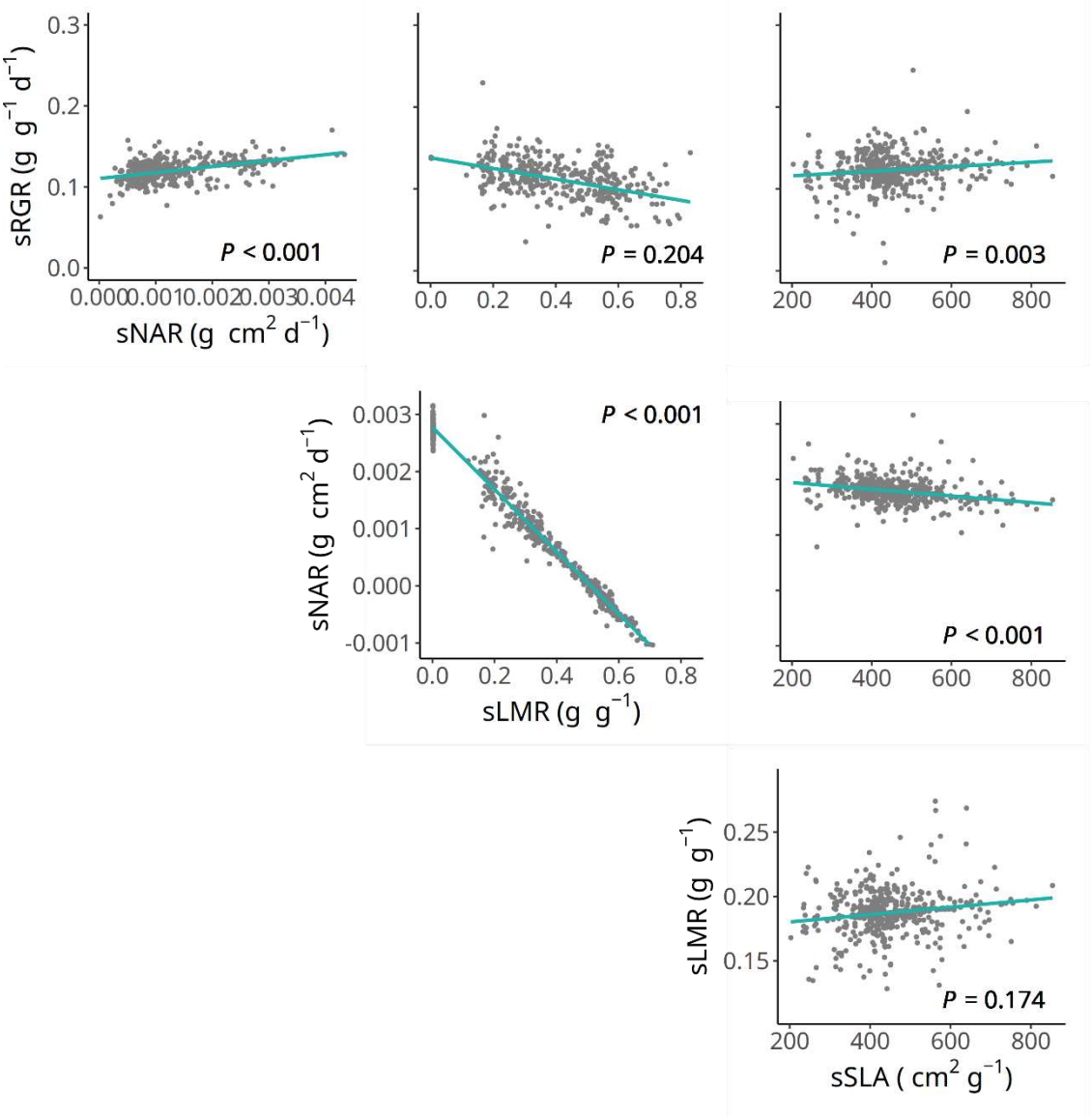


Fig. S5 Partial residuals and prediction line of the linear mixed-effects model showing the relationship between size-specific relative growth rate (sRGR), net assimilation rate (sNAR), leaf mass ratio (sLMR), and specific leaf are (sSLA). For sRGR, linear mixed-effects models included the interaction 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.

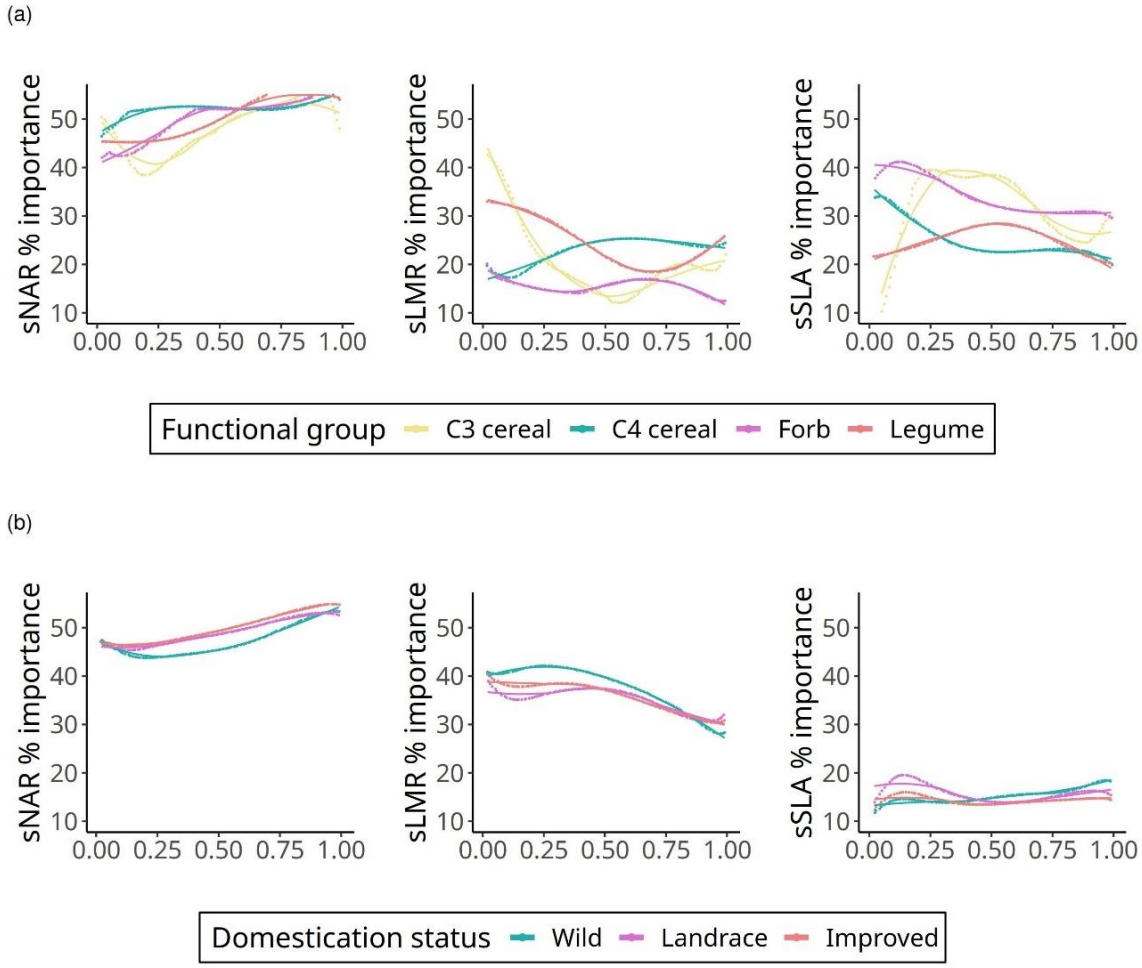
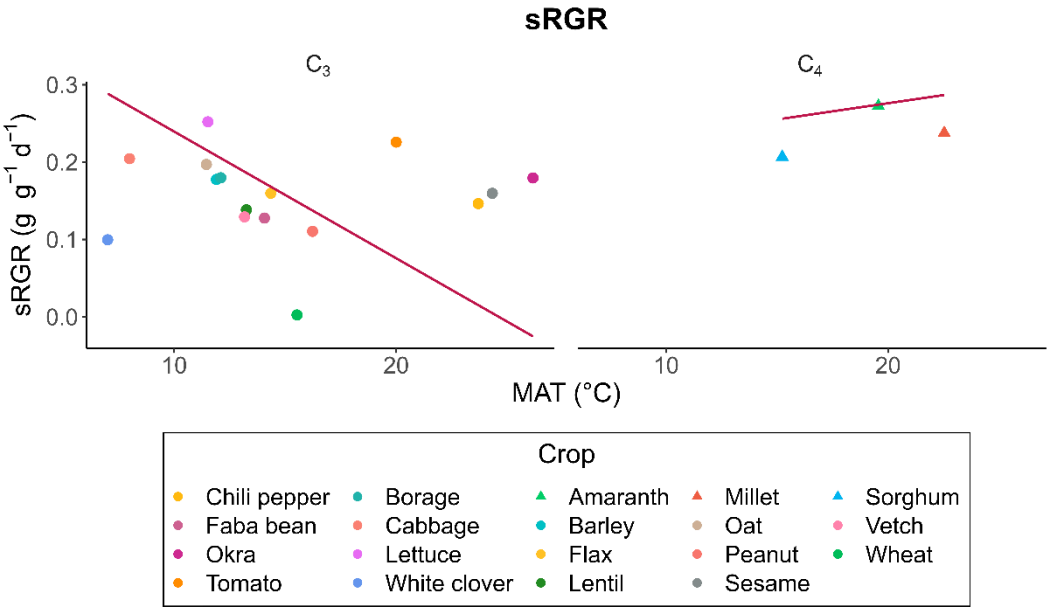


Fig. S7 Mean size-specific relative growth rate (sRGR) as a function of mean annual temperature (MAT) at crop origin and photosynthetic pathway (C_3 *vs.* C_4). Solid lines represent the fitted phylogenetic generalized least squares model (PGLS). Symbols represent the photosynthetic pathway: C_3 (circles)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