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Research review

An allometry perspective on crops

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Summary

Understanding trait–trait coordination is essential for successful plant breeding and crop modeling. Notably, plant size drives variation in morphological, physiological, and performance-related traits, as described by allometric laws in ecology. Yet, as allometric relationships have been limitedly studied in crops, how they influence and possibly limit crop performance remains unknown. Here, we review how an allometry perspective on crops gains insights into the phenotypic evolution during crop domestication, the breeding of varieties adapted to novel conditions, and the prediction of crop yields. As allometry is an active field of research, modeling and manipulating crop allometric relationships can help to develop more resilient and productive agricultural systems to face future challenges.

Introduction

For wild and cultivated species, body size is a key parameter of plant performance, fitness, and yield. Accordingly, plant size, expressed in terms of biomass, diameter or height, has considerably changed during evolution under cultivation (Fig. 1). On the one hand, early domestication and further diversification of landraces and varieties generally enlarged plants and their harvested parts, such as grains, fruits and leaves (Schwanitz, 1967; Evans, 1993; Meyer *et al.*, 2012; Milla & Matesanz, 2017; Gómez-Fernández & Milla, 2022). On the other hand, selection reduces plant height to facilitate fruit tree harvesting and avoids lodging in cereals (Hedden, 2003; Niklas & Marler, 2007). For instance, the introduction of dwarf genotypes in the 1960s by modern breeding enabled a massive increase in cereal yields under high-input agriculture, known as the Green Revolution (Donald, 1968; Khush, 1999; Hedden, 2003). Thus, selection for size has been essential in agriculture, with contrasting (but both successful) size-selection strategies in early and recent historical times.

Body size influences many aspects of organisms' physiology, morphology, and life history (Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1996). In plants, most phenotypic variance in adaptive traits is related to variability in whole-plant size (Díaz

et al., 2016). For instance, many traits related to biomass allocation, metabolic rates, and nutrient stoichiometry vary with global diversity in plant size (Niklas, 1994; Cornelissen, 1999; Aarssen & Jordan, 2001; Reich *et al.*, 2006; Díaz *et al.*, 2016). Moreover, genetic studies revealed that the genes controlling plant size jointly modulate many associated traits (so-called pleiotropic effects; see Guo *et al.*, 2010; Lim *et al.*, 2018). This suggests that trait–size relationships might reflect lines of least resistance along which genetic variation and selection primarily act. In crops, coordinated changes in plant size, morphology, and physiology are observed during the domestication of various species (Evans & Dunstone, 1970; Evans, 1993; Kluyver *et al.*, 2017; Milla & Matesanz, 2017). For example, plant size and harvested organ size tend to show parallel changes between ancestral and selected varieties in different types of crop species (Fig. 1). Consequently, as trait–size relationships have likely shaped current crop phenotypes, understanding them is crucial for predicting the impact of a change in one trait on the whole-plant phenotype during plant breeding. Furthermore, modeling of trait–size relationships in crop species allows us to understand to what extent human-assisted selection of specific crop features, such as high biomass allocation to reproduction, can manipulate trait–size relationships to improve crop performance.

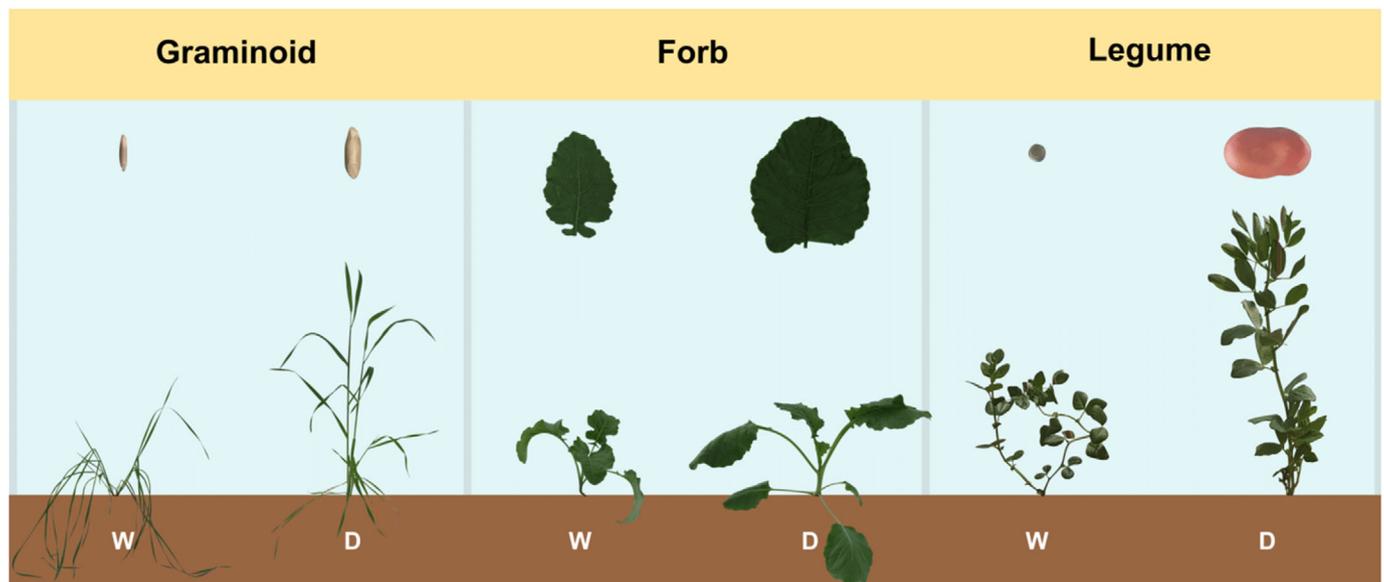


Fig. 1 Simultaneous changes in plant and organ size during crop domestication. Examples of size changes observed in a graminoid, a forb, and a legume crop type. From left to right: wild (W) and domesticated (D) wheat (*Triticum diccocooides* Schweinf., *Triticum durum* Desf.), cabbage (*Brassica oleracea* L.), and faba bean (*Vicia narbonensis* L. and *Vicia faba* L.). Whole-plant images are depicted at a consistent scale, harvestable organs are represented on scales specific to each crop. Further information on accession identities can be found in Gómez-Fernández *et al.* (2022).

In the past century, research into trait variation has revealed that traits often change disproportionately with increases in plant size (McMahon & Bonner, 1983; Schmidt-Nielsen, 1984; LaBarbera, 1989). This phenomenon is known as an allometric scaling relationship where the value of a given trait and size are functionally interconnected. Allometry refers to the proportional changes in the traits of an organism scales or changes in relation to plant size. Mathematically, this relationship between a given trait and size is often expressed as a power function (Huxley, 1924, 1932; Gould, 1966; Niklas, 1994; Calder, 1996) where:

$$Y = \alpha M^{\beta}$$

In this equation, Y is a plant trait that depends on the whole-plant mass M , α is a normalization constant that may vary between individuals or species, and β is the scaling exponent. The value of β is the slope of the relationship after log-linearization and indicates the nature of the trait change with respect to a change in plant mass. It describes whether traits change in direct proportion to body size (i.e. isometrically, $\beta = 1$) or allometrically (i.e. nonlinearly, $\beta \neq 1$) with plant mass. As discussed below, allometry is particularly valuable to crop breeders because it provides insights into how the selection of different traits can influence other traits and plant growth, which is crucial for optimizing crop yield, size, and resource allocation.

In the 1930s Kleiber (1932) observed that the metabolic rate of most animals scales to the $3/4$ of their mass (today known as the 'Kleiber's law'). More recently, a similar scaling relationship between size, growth, and metabolism, has been reported for plants (Enquist *et al.*, 1998, 2000; Niklas & Enquist, 2001). Remarkably, across diverse species and kingdoms, these scaling exponents exhibit a general consistency, often converging around approximate

quarter-power scaling exponents (e.g. $1/4$, $3/4$, $3/8$) (Kleiber, 1947; Banse, 1976; Niklas, 1994; Enquist *et al.*, 2000; Niklas & Enquist, 2001). This intriguing observation suggests that allometric relationships emerge from fundamental properties in the way organisms are built (Elgin, 2006; Sousa *et al.*, 2008; Glazier, 2014; Kempes *et al.*, 2019), which fostered the development of mechanistic theories to explain the seemingly apparent near-universality of many scaling relationships. For example, the surface area theory predicts a $2/3$ scaling exponent for how many traits and attributes, including metabolic rate and growth rate ($2/3$), population density ($-2/3$), and plant height ($2/3$), scale with changes in plant size, as a result of the disproportionate increase in volume with surface area (Rubner, 1883; White, 1981; Niklas, 1995; Dodds *et al.*, 2001). By contrast, the metabolic scaling theory (MST) predicts how numerous physiological and anatomical traits scale with allometric exponents that are multiples of a quarter (e.g. $-1/4$, $1/4$, $3/4$) based on the fractal organization of transport networks in multicellular organisms (Box 1). For instance, MST predicts a $3/4$ scaling exponent for the allometry of plant growth rate, which is consistent with observations across species and reflects that a plant 10 times larger is constrained to grow on average only 5.6 times faster, independently of the species and genotype. Extensions of MST also predict how the metabolic and growth exponent can vary due to differences in the scaling of the vascular network geometry and how this variation then influences the plethora of traits that covary with body size (Price *et al.*, 2007; Enquist & Bentley, 2012).

Statistical regularities in allometry suggest that biophysical laws strongly constrain trait–size relationships. Yet, as these relationships have not been extensively studied in crop species, whether crop traits scale with size as wild species remains unknown. Interestingly, there is a growing number of studies reporting scaling variability across and between species (White, 2010; Kozłowski

Box 1 Metabolic scaling theory

The metabolic scaling theory (MST) has been used to predict many trait–size relationships in plants (West *et al.*, 1997, 1999a,b; Enquist & Niklas, 2002; McCarthy & Enquist, 2007). The predictions of MST are based on the geometry of vascular branching transport systems that evolved in multicellular organisms to deliver nutrients to every metabolic-active cell (West *et al.*, 1997, 1999a). The theory posits that natural selection for energy-efficient nutrient delivery favored the evolution of space-filling, fractal-like transport structures in all multicellular organisms. The key predictions of MST are that, on average, plant growth rate scales isometrically to leaf biomass, ($\beta \approx 1$) and allometrically ($\beta \approx \frac{3}{4}$) with total biomass (Enquist *et al.*, 1998; West *et al.*, 1999b; Price *et al.*, 2007). Furthermore, numerous additional plant anatomical and physiological traits are predicted to covary with β such as plant respiration, photosynthesis, plant height, stem diameter, xylem conduit dimensions, biomass allocation, and plant density (West *et al.*, 1999b; Enquist & Niklas, 2002; Price *et al.*, 2007; Savage *et al.*, 2010; Enquist & Bentley, 2012; Deng *et al.*, 2012b). Many studies have tested MST predictions across plant species, and to a lesser extent, within plant species (Reich, 2001; Reich *et al.*, 2006; Duursma *et al.*, 2010; Vasseur *et al.*, 2012, 2018). These analyses allowed validating model predictions but also documented that some species and taxa deviate from the optimal $\frac{3}{4}$ scaling phenotype and that the scaling exponent for growth rate tends to change from isometric to allometric in small to large plants, across and within plant species (Enquist *et al.*, 2007; Mori *et al.*, 2010; Poorter *et al.*, 2015; Vasseur *et al.*, 2018). Relaxation of MST assumptions of space-filling or branching structure can begin to explain observed deviations from model predictions, suggesting that vascular network geometry can underlie scaling relationships (Enquist, 2002; Price *et al.*, 2007). Testing theoretical predictions with empirical data helps validate or invalidate theory assumptions, informing about the mechanisms shaping allometric relationships in plants.

et al., 2020; Glazier, 2022), and it is becoming increasingly clear that allometry is not only the result of biophysical constraints, but also the result of evolutionary processes such as natural selection (Enquist & Bentley, 2012; Vasseur *et al.*, 2018; Glazier, 2022; White *et al.*, 2022). Consequently, allometric relationships are also expected to respond to human-assisted selection, for instance to improve growth rate and seed yield by the selection of specific scaling parameters.

We advocate that allometric modeling might help understand how targeted outputs can – or cannot – be selected for in crop species. Such an approach has long been utilized in animals (Brody, 1964). Recent allometric studies in animal husbandry, including the domestication of chickens, pigs, and horses have been associated with changes in their scaling relationships (Evin *et al.*, 2015; Sánchez-Villagra *et al.*, 2017; Heck *et al.*, 2019; Núñez-León *et al.*, 2021). Moreover, chicken domestication was related to parallel changes between body, beak, and limb size, and modeling their allometry gave insights to enhance chicken breeds (Núñez-León *et al.*, 2021). In this article, we argue that developing a similar approach in crops can be powerful. First, we evidence that allometric relationships have shaped crop evolution during plant domestication. Then, we highlight to what extent modeling allometric relationships could give new opportunities for crop

improvement. Finally, we discuss how modeling crop allometries can help predict optimal crop performance in the field when grown in monoculture or under diversified conditions.

Evolution of plant allometry over the course of crop domestication

The domestication syndrome entails common phenotypic changes observed during the domestication of several species, such as enlarged harvestable organs, loss of natural seed dispersal, and decreased seed dormancy (Vavilov, 1951; Hammer, 1984; Evans, 1993; Fuller, 2012; Meyer *et al.*, 2012). The domestication syndrome also includes modifications in biomass allocation patterns with crops generally allocating a higher proportion of total biomass to the harvested part than their wild progenitors (i.e. crops have a higher harvest index, Evans, 1993; Hay, 1995; Berrocal-Ibarra *et al.*, 2002; González-Paleo & Ravetta, 2012; Royo *et al.*, 2021). However, as allometric relationships reflect (predictable) changes in biomass proportions with size (Coleman *et al.*, 1994; McCarthy & Enquist, 2007; Weiner *et al.*, 2009; Poorter & Sack, 2012), to what extent shifts in biomass allocation during domestication resulted solely from allometric changes remains an open question (see McCarthy & Enquist, 2007; e.g., the so-called ‘passive’ plasticity, Wang *et al.*, 2020). For instance, Qin *et al.* (2016) found a unique isometric relationship between root and shoot biomass across crop species, as predicted by MST theory (Enquist & Niklas, 2002), suggesting that root : shoot ratio evolved in crops following predictable allometric equations. However, other studies reported changes in plant allometry between wild progenitors and modern varieties in different crop species (Niklas & Marler, 2007; Milla *et al.*, 2014; Pedrosa *et al.*, 2018; Roucou *et al.*, 2018). For instance, significant differences in allometric coefficients of plant diameter-height and seed mass-fruit mass relationships were reported in papaya and Amazon tree grape (Pedrosa *et al.*, 2018), suggesting that domestication and selection altered crop allometries. Although a similar scaling exponent between crops and wild species was also found for the seed mass-seed coat allometry, the lower intercept across crops may have resulted from selection for decreased seed dormancy (Milla *et al.*, 2024).

The impact of domestication on plant growth rate has recently been carefully addressed (Simpson *et al.*, 2017; Gómez-Fernández *et al.*, 2022; Gómez-Fernández & Milla, 2022). These studies showed that the improvement of plant growth rate has not been homogeneous across species, as it depended on their domestication history. However, a re-analysis of published data from 19 crop species revealed that, on average, crop growth rate scales with an exponent indistinguishable from the predicted $\frac{3}{4}$ exponent (Fig. 2a,b), which would suggest similar constraints on the evolution of growth rate. At least, this indicates that crop species do not differ in their scaling from noncrop species and generally conform to the allometric relationship for growth rate predicted by MST. Moreover, wild ancestors, landraces, and elite lines shared a common growth rate-size relationship (Fig. 2b), which suggests that allometry has not been changed upon domestication. Despite a general adherence of crops to the MST prediction, our re-analysis also showed that the scaling exponent varied significantly between

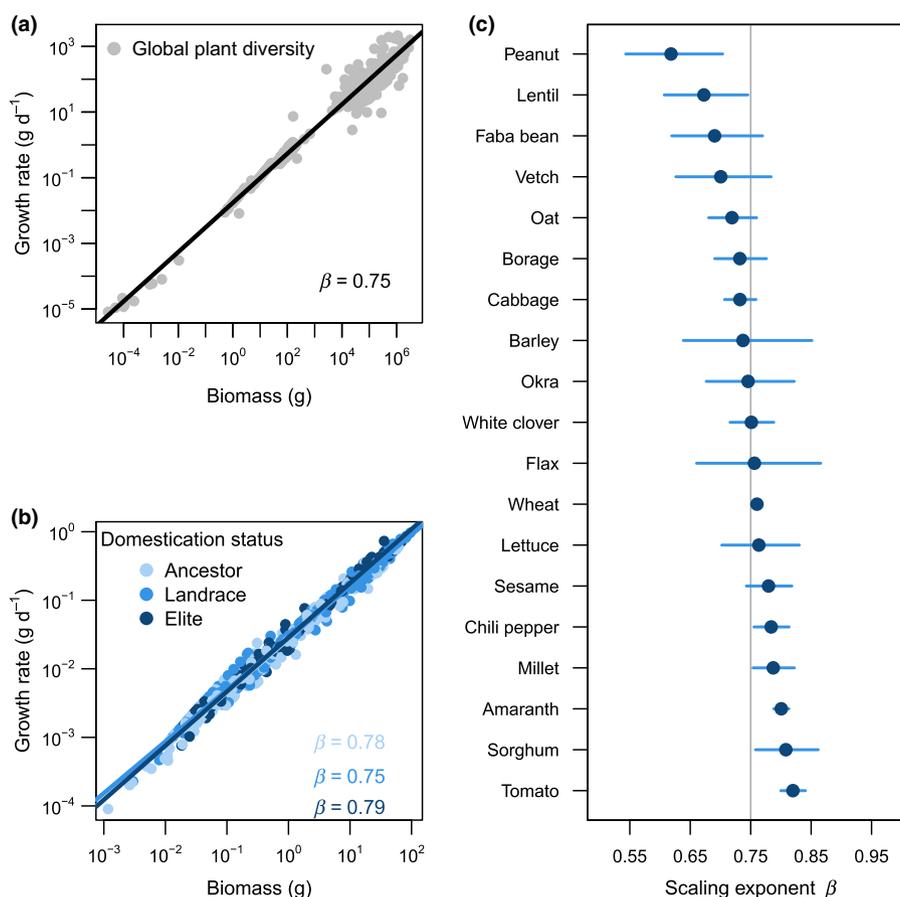


Fig. 2 Variation in crop growth rates explained by scaling relationships. (a) The previously reported scaling exponent (β) of $\frac{3}{4}$ for growth rate across a wide range of plant sizes found by Niklas & Enquist (2001). (b) Allometric re-analysis of the crop growth–plant size relationship at different stages of evolution under cultivation, using the data of 19 crop species from Gómez-Fernández *et al.* (2022). Three main domestication statuses can be distinguished (Abbo *et al.*, 2014; Gómez-Fernández *et al.*, 2022): ancestors, the closest wild relatives; landraces, domesticated genotypes that have not undergone intensive breeding in the last century; and elites, genotypes from more recent breeding programs (post-World War II). For each crop and domestication status, growth and size data were obtained from at least two different accessions representing crop diversity (for more information on accession identities, see Gómez-Fernández *et al.*, 2022). Differences in scaling parameters between wild progenitors, landraces, and elites were not statistically significant. (c) Variation in scaling exponents for the plant size–growth rate relationship between crop species. Crop species were ordered by increasing mean scaling exponent from top to bottom. Crop-specific scaling exponents ($\pm 95\%$ confidence intervals) were calculated by reanalyzing landrace and elite data for each species from Gómez-Fernández *et al.* (2022). The vertical line represents the $\frac{3}{4}$ scaling exponent predicted by the metabolic scaling theory (MST). Allometric analysis was performed with standard major axis tests using the *SMATR* R package (Warton *et al.*, 2012).

crop species around the predicted $\frac{3}{4}$ exponent (from $\frac{2}{3}$ to $\frac{4}{5}$; Fig. 2c). As such, more experimental studies are needed to unveil how crop-specific variations in the scaling exponent relates to crop type and domestication history. Nonetheless, these results indicate that domestication has been strongly constrained by allometry. Together, these findings illustrate that domestication has modified specific allometric relationships, and not all. Whether modern selection can still operate on plant allometries, on which relationships and to what extent, is a critical question for future crop improvement.

Plant allometry: constraint or promise for plant breeding?

Relatively conserved allometric relationships among crop and wild species (as in Fig. 2b) may indicate that trait–size

relationships represent an optimum in the fitness landscape, constraining the evolution of new phenotypes along the allometric line (Olson, 2012). Interestingly, beyond growth rate, allometric theories also make predictions about how traits such as biomass allocation change with plant size. For instance, MST predicts that leaf mass, stem diameter, and root mass scale with whole-plant mass as the $\frac{3}{4}$, $\frac{3}{8}$, and 1, respectively (Enquist *et al.*, 1998, 1999; Enquist & Niklas, 2002). Moreover, power law equations also generally describe allocation to and in reproductive tissues such as seed or fruit weight and their quality in terms of protein, sugar, or nitrogen content (Samson & Werk, 1986; Martre *et al.*, 2003; Niklas & Enquist, 2003; Niklas, 2006; Rotundo *et al.*, 2009; Weiner *et al.*, 2009; Plessis *et al.*, 2013). Often there is no clear prediction for scaling exponents related to reproductive traits, presumably because the associated relationships are more variable and taxon-specific. This questions to what extent biomass

allocation in crops, notably the biomass allocated to the harvested part, can be predicted by allometric theory. The few studies investigating allometric relationships for biomass allocation in crop species found MST-predicted scaling exponents for root–shoot allocation or stem–leaf mass allocation, as observed in wild species (Qin *et al.*, 2016; Milla & Matesanz, 2017). These promising findings open new avenues for predicting optimal crop performance with allometric models. Simple allometric equations could offer a valuable alternative, or complement, to complex crop models requiring many parameters. However, further analyses and experiments are needed to test this approach. One main limitation is that measuring traits related to plant allometry (i.e. size, biomass allocation, and physiological rates at the *individual* level) is experimentally laborious, which prevents comparative studies across a large range of varieties. However, the growing capacities of high-throughput phenotyping facilities combined with technological development (Granier *et al.*, 2006; Flood *et al.*, 2016; Tardieu *et al.*, 2017; Reynolds *et al.*, 2019; Volpato *et al.*, 2021), now leverage our ability to analyze multiple crop species and varieties, which opens the door to the use of allometric models for crop performance prediction. For instance, allometry was recently used to predict fruit development from ovule protein concentration in eight crop species (Colombié *et al.*, 2023).

If allometric relationships are strongly constrained and poorly variable, the range of trait combinations that plant breeders can create and use for varietal improvement might be limited. However, genetic variation at the intraspecific level for scaling parameters has now been strongly documented (Glazier, 2005; Chmura *et al.*, 2017; Careau & Glazier, 2022), which can provide new opportunities for plant breeding. For example, high heritability (broad-sense $H^2 = 0.95$) for variation in the growth rate–size scaling exponent was found in the plant *Arabidopsis thaliana* (Vasseur *et al.*, 2018). In addition, recent works suggest that variation in the scaling exponent is associated with variation in plant performance and stress resistance (Muir & Thomas-Huebner, 2015; Vasseur *et al.*, 2018). In *A. thaliana*, deviations from $3/4$ scaling decreased seed production and increased stress resistance (Vasseur *et al.*, 2018). Is variation in scaling exponents among crop varieties similarly associated with the optimization of different components of performance? Answering this question might become critical to adapt crop varieties to future climate. Allometric engineering, that is experimentally changing scaling parameters, has been proposed to test the impact of allometric deviation on performance (Sinervo & Huey, 1990; Olson, 2012). In addition, artificial selection experiments on allometric parameters are expected to be a powerful approach to test the links between scaling variation and fitness traits, its genetic architecture, and its response to selection (Conner, 2003; Frankino *et al.*, 2005; Egset *et al.*, 2012; Pélabon *et al.*, 2014; Voje *et al.*, 2014; Bolstad *et al.*, 2015; Houle *et al.*, 2019). For instance, increased yields during recent plant breeding have been accompanied by a modulation of allometric relationships for biomass allocation in soybean (Tamagno *et al.*, 2020), oats (Semchenko & Zobel, 2005), and wheat (Qin *et al.*, 2013). We firmly believe that investigating the links between allometric variation and yield has a great power

for crop improvement and crop modeling. We highlight below possible avenues in that direction.

First, we need to screen for genetic variation in allometric parameters by analyzing trait–size variation at a particular phenological stage, during ontogeny or in response to environmental gradients (Fig. 3). For instance, by examining the residuals of the relationships, we can analyze allometric variation as the departure of peculiar genotypes from the global allometric relationship (Fig. 3, middle panel). Moreover, if the allometric relationship exhibits nonlinearity after log-linearization, which has been frequently reported across and within species (Enquist *et al.*, 2007; Kolokotronis *et al.*, 2010; Mori *et al.*, 2010; Vasseur *et al.*, 2012, 2018; Poorter *et al.*, 2015; Zhou *et al.*, 2021), this indicates variation in slopes (i.e. in allometric exponents) between genotypes (Fig. 3, middle panel). Quadratic models better fit nonlinear allometric relationships, and the derivative of the model measures the variation of allometric exponent between genotypes (Kolokotronis *et al.*, 2010; Vasseur *et al.*, 2018). As higher scaling exponents reflect a more-efficient trait increase per unit biomass, investigating such intraspecific variation may be critical to improve future crop varieties. As many traits vary dynamically with size during development (such as biomass allocation see McConaughay & Coleman, 1999; Poorter & Sack, 2012), allometric models can be used to detect genetic variation for trait trajectories during ontogeny or in response to the environment (Ma *et al.*, 2002; Long *et al.*, 2006). The use of allometric models allowed to identify many quantitative trait loci (QTL) regulating biomass allocation patterns during ontogeny, including stem and seed mass (Li *et al.*, 2007; Huang *et al.*, 2014; Jiang *et al.*, 2016). As such, breeders can select for genotypes having more or less ‘stable’ trajectories during the season (Fig. 3, right panel), which may be interesting to govern yield stability. In addition, genotypic responses to an environmental gradient can be analyzed from an allometric perspective. For instance, when different genotypes are grown in contrasting levels of resource availability, this will impact their size and traits following scaling equations (Fig. 3, right panel). Indeed, it is known that allometric parameters may change between different environments, such as with water (Eziz *et al.*, 2017) or nutrient availability (Semchenko & Zobel, 2005; Li *et al.*, 2017). The parameters of these equations determine allometric reaction norms, which inform about the sensibility of a genotype to a particular environmental stress. For instance, changes in plant density revealed genotype-specific allometries for reproductive allocation in wheat, maize, soybean, and sunflower, informing how the harvest index changes with plant density (Vega *et al.*, 2000; Weiner *et al.*, 2009; Qin *et al.*, 2013; Du *et al.*, 2020). Therefore, allometric models have the power to jointly compare the traits of genotypes in optimum conditions and in response to stress. As a proof of concept, recent studies characterized genetic variation for shade-avoidance responses in wheat by studying allometric slopes (Zhang *et al.*, 2023; Golan *et al.*, 2024). Altogether, different methods can be used to screen for genetic variation in scaling parameters affecting different components of crop yield.

Second, we need to resolve the genetic determinants of trait–size relationships and allometric coefficients. The genetic determinism of allometric relationships recently started to be elucidated, but the

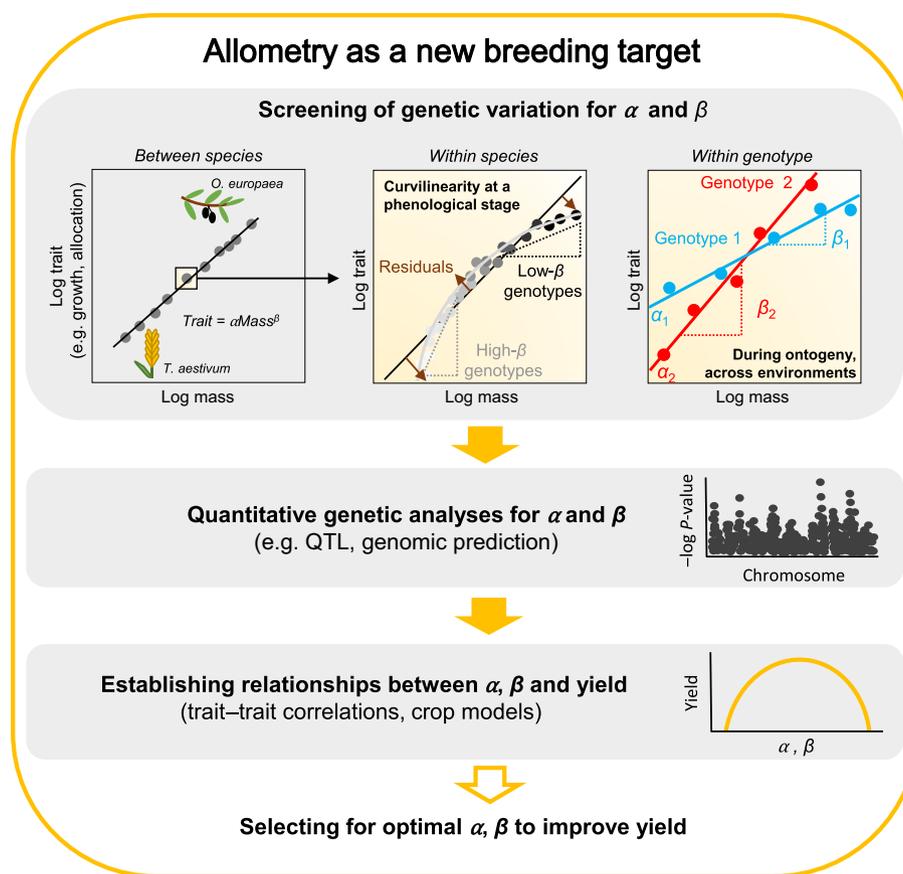


Fig. 3 Allometry as a new breeding target. Three-step framework outlining how to use intraspecific allometric variation as a breeding target. First, trait–size variation is screened across and within species. Across species (left panel), allometric relationships are continuously tested with trait–size data in wild and cultivated species to analyze the adherence of species to global patterns in trait–size variation. Within species (middle panel), a population of genotypes is screened for variation in scaling parameters – normalization constant (α) and scaling exponent (β) – of a given trait. For example, trait–size variation within a species often shows nonlinearity at a particular phenological stage (also called static allometry by Cheverud, 1982; see Vasseur *et al.*, 2012, 2018). Next to scaling parameters, the residuals of the relationships can be analyzed as the departure of genotypes from the global allometric relationship (middle panel, see Wuest *et al.*, 2022). Within genotypes (right panel), scaling relationships during growth (so-called ontogenetic allometry, Li *et al.*, 2007) or in response to environmental conditions (Qin *et al.*, 2013; Du *et al.*, 2020) may vary between genotypes. For example, impaired growth in sub-optimal conditions leads to reduced trait value, such as allocation to reproduction being less strongly in genotype 1 (blue line) than in genotype 2 (red line). After screening of allometric variation between genotypes, genetic association studies can be carried out in order to identify underlying genomic determinants, for example quantitative trait loci (QTL) or SNPs, and genetic architecture (Li *et al.*, 2007; Plessis *et al.*, 2013; Huang *et al.*, 2014; Vasseur *et al.*, 2018; Zhang *et al.*, 2020). Finally, the impact of scaling variation in α and β on performance (yield and its components) can be evaluated in the field (including effective field networks) or with allometry-enriched crop growth models (Messina *et al.*, 2011; Vasseur *et al.*, 2018). Together, genetic determinants of allometric parameters and their relationships with yield can be manipulated and/or used in gene-to-phenotype models during the breeding process that now explicitly incorporate allometry as a breeding target.

molecular mechanisms of coordinated changes in size and traits still need to be investigated (Vasseur *et al.*, 2022). Quantitative analysis of genetic variation in allometric coefficients offers a promising avenue to help breeders to identify genes that modulate yield, productivity, and competitiveness through allometric relationships. For instance, single-nucleotide polymorphisms (SNPs) have been identified explaining coordinated changes in plant and organ size (Guo *et al.*, 2010; Lim *et al.*, 2018; Vicente *et al.*, 2023), such as seed weight and plant height in barley (He *et al.*, 2023). It has been argued that scaling relationships at whole-plant level may be controlled by mechanisms operating at lower organizational levels, generating allometries from cell size to whole-plant size (Bennett, 1987; Gregory, 2002; Kozłowski *et al.*, 2003; Starostová

et al., 2009; John *et al.*, 2013; Mueller, 2015; Roddy *et al.*, 2020; Bestová *et al.*, 2021). Interestingly, genes controlling cell size, such as transcription factors (e.g. YABBY, MYB, and bHLH) influenced yield-related traits in crop species (Cong *et al.*, 2008; Wilkins *et al.*, 2009; Nicolas *et al.*, 2013; Lim *et al.*, 2018). Cell size was also related to enlarged organ size during domestication as a result of genome-doubling by polyploidization (Dunstone & Evans, 1974; Evans, 1993; Fang & Morrell, 2016; Salman-Minkov *et al.*, 2016). Indeed, positive scaling relationships between cell and genome size have been described across plant species (Mowforth & Grime, 1989; Kozłowski *et al.*, 2003; Knight & Beaulieu, 2008), but not yet at the intraspecific level. Interestingly, genome size variability was related to leaf traits in maize (Tenaillon *et al.*, 2011; Díez

et al., 2013), suggesting that scaling relationships at lower levels of organization influence trait variation at higher levels within species. Our growing understanding of the genetic determinism of allometric relationships paves the way for selection on scaling parameters as a way to manipulate the additive genetic values of growth rate, biomass allocation, and stress resistance. Moreover, allometric models can also be useful to improve the breeding of hybrids, which have long been key agronomical innovations in agronomy (Box 2).

Third, we need to evaluate the impact of scaling variation on crop performance in field conditions (Fig. 3). Increased scaling exponents for reproductive allocation in soybean varieties released between 1980 and 2013 (Tamagno *et al.*, 2020) suggest that scaling exponent variation may have been used by breeders to improve previous yields. Until now, how scaling parameter variation links to field performance is unknown. However, in cereals, genetic

variation in allometric coefficients has been related to yield stability across environments (Du *et al.*, 2020; Weiner *et al.*, 2021): A low scaling exponent (Fig. 3, blue line) may have greater yield stability compared with a high scaling exponent (Fig. 3, red line). In addition to correlation of scaling variation with performance, allometry-enriched crop growth models may be used to predict the impact of scaling variation on yield. After the evaluation of scaling variation on crop performance in the field, genomic prediction methods can be used to predict genotypic values for alpha and beta (Fig. 3) and assist in selecting those genotypes with the best set of scaling parameters for success in a given environment.

Scaling up to crop field performance

Allometric models have been developed to scale up from individual traits to population- and ecosystem-level features (Brown

Box 2 Prediction of hybrid vigor using allometry

Hybrids are expected to exhibit higher growth, disease resistance, and fertility than their parents (Crow, 1998). This phenomenon, called hybrid vigor or 'heterosis', is widely observed and agronomically exploited in plants and animals (Chen, 2010). Heterosis is quantified by the phenotypic deviation of a hybrid compared with the mean or best parental value, reflecting the nonadditive inheritance of the trait. However, the underlying mechanisms continue to puzzle biologists. As early as 1934, Wright proposed a model based on trait relationships to explain the metabolic deviation of hybrids at the cellular level. Wright's model was based on the relationship linking the concentration of enzymes to the metabolic flux that integrates their activity. Given that this relationship is nonlinear, the metabolic flux is expected to deviate ($Y_{Aa} > Y_{\text{mean}}$, Fig. 4) even if enzyme concentrations are additively inherited ($M_{Aa} = M_{\text{mean}}$). Recently, Fiévet *et al.* (2018) validated this approach by demonstrating that the enzyme–flux relationship can be modelled to predict hybrid variability for glycolysis in yeast. Interestingly, Wright tackled the problem of heterosis by exploring the geometry of trait relationships at different levels of phenotypic integration. Indeed, Wright's model suggests that hybrid deviation can be quantitatively explained by the curvature of trait relationships between two levels of phenotypic integration (also called Jensen's inequality). However, this approach has been completely ignored in studying complex trait inheritance in plants, such as those related to crop yield. This is mainly because, until recently, we lacked a mathematical framework to model complex trait variation and covariation. Yet, allometric models of trait relationships have considerable promise to scale up Wright's model of hybrid deviation to higher integration levels.

Due to the nonlinearity of allometric relationships (when traits are not log-transformed; solid black line, Fig. 4), the hybrid is expected to exhibit a higher Y value than predicted from a linear relationship (dashed black line), assuming additive inheritance for plant biomass. For instance, growth–size relationships were successfully used to predict the heterosis in *Arabidopsis thaliana* hybrids (Vasseur *et al.*, 2019). This case study in a model species suggests that testing the ability of allometric relationships to explain and predict hybrid vigor in crop plants represents a critical challenge to accelerate varietal improvement and optimize field performance in the near future.

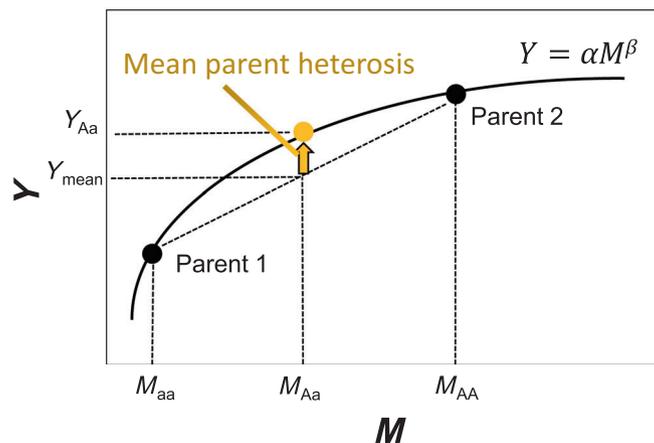


Fig. 4 Using nonlinearity of allometric relationships to predict mean parent heterosis. The nonlinear relationship between a trait (Y) and plant size (M) enables to predict mean parent heterosis in Y in the offspring (M_{Aa}) of a cross between two parents (M_{aa} , M_{AA}). The figure is based on the model presented in Vasseur *et al.* (2019).

Box 3 Allometry in crop models: current usage and future promises

Crop models are built to simulate plant growth, development, and yield under various field conditions (Monteith, 1977; Brisson *et al.*, 2003; Jones *et al.*, 2003; Keating *et al.*, 2003; Soltani *et al.*, 2013; Chenu *et al.*, 2017; Messina *et al.*, 2022). Mechanistic crop models typically use climatic variables to simulate plant processes such as temperature to simulate leaf area development that, in turn, determines how much light is transformed into biomass. Then, the developmental stage or a trait–size relationship determines how biomass is distributed to roots, leaves, stems, or grains (Marcelis *et al.*, 1998). For instance, trait–size relationships are used by the SSM-iCrop model to predict biomass allocation to leaves (Soltani *et al.*, 2013) and by the APSIM model to predict the number of grains (Zheng *et al.*, 2014). However, these trait–size relationships have until now not been linked to the field of plant allometry and mechanistic theory such as for biomass allocation by the metabolic scaling theory (MST, Niklas & Enquist, 2002; Enquist & Bentley, 2012). In addition, emergent trait–size properties from existing crop growth models could be compared with theoretical expectations of MST to test their consistency (Peaucelle *et al.*, 2019). For example, modeling how different plant sizes or densities impact biomass yield could be compared with their MST predictions. Next, allometric relationships may simplify current crop models due to their low parameter number, responding to the demand for parsimonious models to facilitate high-speed simulations (Hammer *et al.*, 2019). As such, allometric relationships for traits such as phenology (Marba *et al.*, 2007; Fournier *et al.*, 2020) and plant density (Deng *et al.*, 2012b) could be integrated to create allometry-enriched crop growth models. Subsequently, genetic variation in scaling parameters can be used to parametrize these allometry-enriched crop models to predict genotypic performance (see Fig. 3). For example, cultivar-specific allometric models between leaf, stem mass, and branch cross-sectional area are used to predict growth and reproduction in mango (Normand & Lauri, 2012). The coupling of genetic analysis (e.g. genomic prediction) with allometry-enriched crop models creates integrative gene-to-phenotype models that can efficiently predict crop performance in multiple environments (Hammer *et al.*, 2006, 2010; Messina *et al.*, 2009, 2022; Technow *et al.*, 2015; Diepenbrock *et al.*, 2022; Onogi, 2022). As variation in a single scaling parameter can drastically impact plant performance, they represent an effective and parsimonious set of parameters to predict the performance of thousands of genotypes across many years and locations within a short time span. Together, we anticipate that an allometry perspective can complement mechanistic crop models to foster the development of high-speed crop models directing crop management and breeding efforts.

et al., 2004; Price *et al.*, 2010). Even if the mechanistic bases are still unclear, the scaling up from individual to ecosystem also displays statistical regularities, which offers testable predictions regarding resource allocation and yield optimization in different management scenarios. For example, the density of organisms per unit area scales with organism body mass (M) following a power law equation with a scaling exponent that is either $c. -2/3$, based on the surface area theory, or $-3/4$, based on MST (White, 1981; Deng *et al.*, 2008). This size dependency of plant density is known as the self-thinning rule (White, 1981). Furthermore, MST predicts that standing biomass per unit land area increases as $M^{1/4}$ and canopy growth as M^0 (Enquist *et al.*, 1998; Brown *et al.*, 2004). These

equations are used to predict features of ecosystems that were previously inaccessible such as how forests influence global carbon and water cycles (West *et al.*, 2009; Coomes *et al.*, 2012). Recently, MST predictions for density and biomass production were empirically confirmed across a range of crop species and allowed to determine the optimal density to maximize biomass yield (Deng *et al.*, 2012a,b). Allometric relationships were also used to determine nitrogen fertilization rate in crops (Sadras & Lemaire, 2014; Lemaire *et al.*, 2019) or to quantify plants' stress levels (Anfodillo *et al.*, 2016). This suggests that allometric models can be used at farm level to aid in decision-making. However, although existing crop growth models already use allometric relationships, allometry remains limited to crop models until now (Box 3). We propose to extend the framework of Deng *et al.* (2012a) with allometric relationships for biomass allocation to predict grain yield. In Box 3, we review how crop models currently use plant size relationships and describe how allometric theory and scaling parameter variation can facilitate the modeling of crop performance in the field.

Adaptive variations that optimize yield at the field level can be associated with different size-selection strategies. In most species, higher plant size is expected to be associated with higher reproductive output. Accordingly, larger and more competitive plants have been selected during domestication and early evolution under cultivation (Milla *et al.*, 2014; Montazeaud *et al.*, 2020). However, as bigger plants compete more with each other (Violle *et al.*, 2009), smaller and less competitive plants can also improve the group's performance (Donald, 1968; Jennings & de Jesus, 1968; Weiner *et al.*, 2010). For instance, selection for communal traits such as shortened stems contributed to yield increases during the Green Revolution and recent varietal improvement (Anten & Vermeulen, 2016; Perez *et al.*, 2019; Weiner, 2019). Furthermore, more vertically oriented leaves reduce the individual plants' competitive ability but avoid light saturation and enable higher photosynthesis in the plant's lower leaves, thereby improving light-use efficiency at the canopy level (Zhu *et al.*, 2010; Perez *et al.*, 2019; Messina *et al.*, 2023). Accordingly, recent plant breeding efforts aim to breed against natural selection for competitive genotypes to increase yield at the population level (Weiner, 2019; Montazeaud *et al.*, 2020). In Box 4, we propose an MST-inspired framework to evaluate how plant breeding for communal traits may have impacted the allometry between size and plant density to increase yield during the Green Revolution. Using such a framework might help understanding which traits facilitated previous yield increases, as well as which factors impacting the size–density relationship allows maximizing crop yield in different species.

Allometry perspective for crop diversification: genotype combination, intercropping, and crop mixtures

Cooperating phenotypes are expected to be particularly efficient under high-density monoculture systems, but less under more diversified conditions. This is because cooperating plants, such as communal plant types that increase light-use efficiency, allowing

Box 4 The Green Revolution through the lens of allometry theory

During the Green Revolution, agricultural yields almost tripled because of the large-scale use of fertilizers and the adoption of high-yielding varieties. These high-yielding varieties were short-statured and had vertically oriented leaves following Donald's ideotype (Donald, 1968). Here, we show how allometric theory can be used to quantify the importance of each driver of increased yield during the Green Revolution.

The total crop yield per unit area is the product of plant density and yield per plant (Deng *et al.*, 2012b):

$$Y = N_{\max} M_{\text{yield}} \tag{Eqn 1}$$

where Y represents the total crop yield produced per unit area that depends on plant density N_{\max} and yield per plant M_{yield} . Metabolic scaling theory (MST) can be used to derive the predicted size–density relationship from the equation of total resource use, which is the product of the number of individuals and resource use per individual (Enquist *et al.*, 1998; Brown *et al.*, 2004):

$$R = N_{\max} Q \tag{Eqn 2}$$

where R is the total resource-use or supply that depends on density N_{\max} and resource-use per plant Q . As the resource-use per individual is predicted to be proportional to growth, $Q \propto M^{3/4}$, this gives (Fig. 5a):

$$R = N_{\max} b_0 M^{3/4} \tag{Eqn 3}$$

$$N_{\max} = \frac{R}{b_0} M^{-3/4} \tag{Eqn 4}$$

where maximal plant density N_{\max} depends on plant size M through a scaling exponent equal to $-3/4$, the resource required for positive growth per unit biomass b_0 , and resource input R . Higher R or lower b_0 results in a higher number of individuals N_{\max} that can be grown per unit area. The yield per plant depends on biomass allocation to the harvestable part and can generally be modelled by an allometric relationship (Pearsall, 1927; Enquist & Niklas, 2002; Niklas & Enquist, 2003; Weiner *et al.*, 2009):

$$M_{\text{yield}} = \alpha M^{\beta} \tag{Eqn 5}$$

where M_{yield} represents the yield per plant that depends on plant size M through a scaling exponent β and a normalization constant α . MST predicts scaling exponents for many vegetative tissues for example $1/4$, $3/4$, for shoot and leaf respectively (Enquist & Niklas, 2002), whereas the scaling exponent for reproductive allocation has no theoretical prediction, varying strongly between species (Weiner, 2004; Weiner *et al.*, 2009).

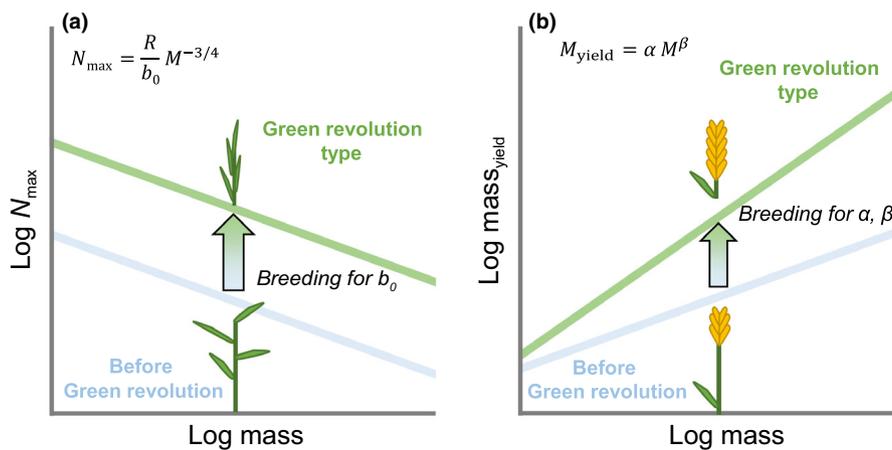


Fig. 5 An allometry perspective on the impact of plant breeding during the Green Revolution. (a) The relationship between plant density (N_{\max}) and plant size (Mass, M) is modelled by an allometric relationship with $-3/4$ scaling exponent β (Deng *et al.*, 2012a,b). Reducing plant resource needs for growth reduces the resource required for positive growth per unit biomass (b_0), thereby increasing maximal planting density for a given plant size. For example, selection for plants with more erect leaves and shorter stems are less competitive and may have allowed increasing plant density and yield during the Green Revolution. Increasing the resource inputs (R) can also increase the number of plants for a given plant size. (b) Plant breeding may also have increased the allocation of biomass to the harvested plant parts by changing the parameters of the allometric relationship (normalization constant α , scaling exponent β) for allocation to the harvested parts (M_{yield}).

This crop model can be used to test how introducing high-yielding varieties and high resource inputs increased yields during the Green Revolution. For example, the introduction of high amounts of artificial fertilizer increased R thereby permitting a higher plant density per unit area (Eqn 4). Breeding for low-competitive genotypes may also have increased plant density by reducing b_0 (Fig. 5a). This may be the case for maize in which yield improvement has been fostered by selecting for density-resistant cultivars with higher light-use efficiency while maintaining the harvest index (Fig. 5a; Duvick, 2005; Lee & Tollenaar, 2007; Perez *et al.*, 2019). The introduction of semi-dwarfs improved biomass allocation to the harvested parts in wheat (Waddington *et al.*, 1986; Evans, 1993; Hay, 1995). This may result from a change in M in combination with a nonlinear relationship with size (Weiner, 2004; Weiner *et al.*, 2009) or by modification of the values of the allometric relationship for biomass allocation (Fig. 5b). A comparison of M , b_0 , α , R , and β across historical series of plant varieties would inform on the relative importance of management vs plant breeding during the Green Revolution. This approach can be extended to evaluate the drivers of yield in other agricultural systems.

a higher plant density per unit area, are susceptible to the invasion of competitive genotypes, known as the tragedy of the commons (Hardin, 1968). Yet, mixing varieties or species in the field may optimize resource uptake and has therefore been proposed to increase yield (Lin, 2011; Litrico & Violle, 2015; Chen *et al.*, 2021). For instance, combining genotypes with different rooting depths may reduce competition for water and nutrients. However, it remains difficult to predict which combination of varieties or species can optimize yield by reducing competition and avoiding the tragedy of the commons. Interestingly, intercropping increased the scaling exponent of reproductive allocation compared with the species in monoculture, resulting in higher allocation rates for larger-sized plants (Gaudio *et al.*, 2021). This suggests that we can improve the reproductive output of one species at a given size when intercropped. As a result, we advocate that allometry can be used to identify the plant sizes for which intercropping is negative, neutral, and positive for reproductive allocation for a species. Importantly, larger plant sizes of the focal species were associated with smaller plant sizes of the associated species (Gaudio *et al.*, 2021). This suggests strong hierarchical competition and may reduce total yield as growing individuals of similar size yields generally higher reproductive mass than growing individuals of very different sizes (Simonsen *et al.*, 2014; Anten & Chen, 2021). Interestingly, the nonlinearity of allometric relationships for reproductive allocation and the associated phenomenon called Jensen's inequality (a recurrent principle as illustrated in Box 2) were used to explain the higher yield in similar-sized individuals (Simonsen *et al.*, 2014; Anten & Chen, 2021). Indeed, increased uniformity between plants of the same genotype has been proposed as a breeding target to increase yield in adverse environments (Borrás & Vitantonio-Mazzini, 2018). These results indicate that large size differences between species or genotypes (i.e. strong hierarchical competition) may increase individual yield of one species but reduce population yield. Thus, using allometry gives insights into the assembly rules of more resource-use-efficient crop cultures.

Conclusion

Assuming that plant size is a major driver of performance at the plant and population level, we advocate here that an allometry perspective on crops is an encouraging avenue for plant breeding and crop modeling that awaits further validation and application.

First, continuing documentation of trait–size relationships, specifically for reproductive traits, at different taxonomic scales will show how allometry shaped crop domestication, and can help identify and predict future evolutionary trajectories (Messina *et al.*, 2011; Milla *et al.*, 2015; Stetter, 2020). Second, studying scaling relationships at the intraspecific level will inform us about the environmental and genetic influences on scaling variation, and will further our capacity to link this variation to performance in the agricultural environment. Finally, a better understanding of crop allometry will allow us to predict yield-related features, such as additive genetic values, heterosis, optimal plant density, and fertilization requirements, thereby helping farmers and breeders in decision-making. Most importantly, we need to perform meta-analyses on a large number of crop species to understand how allometric relationships limit crop evolution. We expect that recent advances in genotyping and phenotyping capacities will allow us to describe scaling relationships and their genetic determinants at different organizational levels. Next, scaling relationships may allow developing complete but simple genotype–phenotype models to predict efficiently plant performance across multiple environments. Moreover, as we still understand limitedly the effects of selection on allometry (Pélabon *et al.*, 2014; Houle *et al.*, 2019), especially in plants, the evaluation of allometries within human-selected crop species is a priority to improve theory and understand the boundaries of phenotypic evolution, a critical question in evolutionary biology (Maynard Smith *et al.*, 1985; Arnold, 1992; Pigliucci, 2007).

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Competing interests

None declared.

Author contributions

AJW wrote the paper with the help of FV, DV and CV. DP, BJE, RM and AG-F provided feedback.

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