Life history variation as a model for understanding trade-offs in plant-environment interactions

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ABSTRACT

All plants must allocate limited resources to survival, growth, and reproduction. In natural species, allocation strategies reflect trade-offs between survivorship risk and subsequent fitness benefits and are therefore central to a species' ecology. Artificial selection on allocation generated high-yielding crops that often invest the bare minimum in defense or longevity. Ecological, genetic, and evolutionary analyses of plant life history -- particularly with respect to longevity and resource allocation along an axis from annual to perennial species -- provides a framework to evaluate trade-offs in plant-environment interactions in natural and managed systems. Recent efforts to develop new model plant systems for research and to increase agricultural resilience and efficiency by developing herbaceous perennial crops motivates our critical assessment of traditional assumptions regarding differences between annual and perennial plant species. We review our present understanding of the genetic basis of physiological, developmental, and anatomical differences in wild and crop species and reach two broad conclusions. First, that perenniality and annuality should be considered syndromes comprised of many interacting traits and that elucidating the genetic basis of these traits is required to assess models of evolution and to develop successful breeding strategies. Modern phenomic and biotechnology tools will facilitate these enquiries. Second, many classic assumptions about the difference between the two syndromes are supported by limited evidence. Throughout, we highlight key knowledge gaps in the proximate and ultimate mechanisms driving life history variation and suggest empirical approaches to parameterize trade-offs and to make progress in this critical area of direct relevance to ecology and plant performance in a changing world.

KEYWORDS

annual, crops, grasses, iteroparity, life history, perennial, semelparity, allocation

INTRODUCTION

Organisms display an extraordinary diversity of strategies to survive the range of environments available on Earth. Life history theory seeks to explain how evolution shapes key components of these organismal strategies to optimize reproductive output against the backdrop of an environment's many predictable and unpredictable factors. An organism's life history comprises its size at birth, rate and pattern of growth, age and size at maturity, the time of reproduction along with the number and size of offspring produced, and various aspects of senescence and duration of life [1]. Several of these, particularly growth rate and reproductive allocation, are important breeding targets for crop and livestock improvement. Components of life history also influence aspects of an organism's ecology, including population size and interactions with other species [2]. Strong correlations exist between life history traits and are often interpreted in the context of selective constraints: evolution may not favor particular combinations of traits. An essential concept in life history theory is that trade-offs occur between resource investment in one trait at the expense of others [3]. Understanding the genetic basis of trade-offs and how they shape ecological strategy or agronomic potential is therefore of central importance for evolutionary biology [4], and for agricultural improvement in a rapidly changing world [5, 6].

Plants vary considerably in their relative resource allocation to growth, reproduction, defense, and storage with two extremes: *annual species*, which tend to reproduce once and then die, and *perennial species*, which delay reproduction past the first season or reproduce over multiple seasons, often with interim periods of quiescence. The majority of calories consumed by humans, both directly or via grain-fed animals, begin as photosynthate captured by annual plants including maize, wheat, soy, and rice [7]. Most molecular and physiological studies likewise employ annuals (e.g. [8]). In recent years, the prospect of developing perennial crops has received attention as a means to reduce agricultural inputs, maintain soil health, and increase diversity in cropping systems [9]. There are now active programs aiming to breed perennial wheat, rice, sunflower, maize, and sorghum, among others [10]. The motivation for developing perennial cropping systems arises from the observation that, as compared to annual relatives, perennial species may be more stress-tolerant and resource-use efficient and may promote soil health via reduced mechanical tilling [9]. (We here focus on herbaceous plant species; the overwhelming majority of woody species are, of course, perennial, as well.) More generally, trade-offs in resource allocation are central to nearly all aspects of fundamental and applied plant science [11]. As one example, nutrients used to mount a constitutive defense against herbivores cannot be used for reproduction, thus reducing fitness in natural settings and yield in agriculture settings in the absence of such stressors.

In spite of the growing interest in developing perennial cropping systems, little recent research has been directed towards understanding the fundamental genetic, physiological and developmental differences, if any, between herbaceous annual and perennial species. Here, we use plant life history variation along an axis from annual to perennial habit as a means to explore trade-offs in resource allocation and consider these trade-offs in the context of the evolution of life histories as well as the prospects for perennial crop breeding. We first identify the components of perennial *versus* annual strategies and evaluate classic assumptions about differences between the two types in their growth, anatomy, rates of resource acquisition, and relative investment in source and sink organs. Throughout, we present the case that perennialty, annuality, and intermediate forms are *syndromes* comprised of many traits. We assess the extent to which constituent traits are functionally integrated and ask whether they are under genetically independent control. While some breeding programs target perenniality *per se* as a breeding goal, we present the case that life history syndromes likely evolved on a trait-by-trait basis and we argue that breeding for only specific components of perenniality may prove more fruitful in the long term. Specifically, by assessing the physiological integration and genetic segregation patterns of individual life history traits, breeders might select desirable combinations of both "annual" and "perennial" traits.

WHAT ARE THE UNDERLYING COMPONENTS OF PERENNIALITY?

Phenology

There exists a broad diversity of phenological patterns within herbaceous perennial taxa (Fig 1). For example, some species persist in a non-reproductive vegetative stage year-round and may have multiple flowering periods per year, as is often observed in wet-tropic perennials. Other perennial herbs common to environments with pronounced seasons have a single reproductive phase per year. In these latter species, the above ground tissues tend to die back annually with winter frost or summer heat and aridity, while the below ground crown and root system persist to facilitate resprouting [12]. The environment, in general, plays an important role in the phenology of plants. For example, compelling evidence links precipitation to phenological shifts in Mojave Desert ecosystems where, despite their unpredictable timing and intensity, autumn rain events clearly trigger mass germination of annuals and also vegetative growth and consequently spring reproductive growth in perennials [13]. Light intensity may also influence phenology as when, for example, the perennial herb *Senecio integrifolius* flowers earlier when exposed to full sun as compared to conspecifics growing under shade [14]. Finally, temperature influences phenology, as many species require exposure to cold (*i.e.,* vernalization) or accumulated days of warmth to germinate or transition to reproduction [15]. These relationships between phenology and environment suggest that the environment triggers shifts in life stage. However the degrees to which environment *versus* genetics contribute toward phenology is not well known in perennials and, indeed, is understood for only a few annuals and biennials [16].

<u>*Meristem determinacy*</u>

Plant meristems determine patterns of vegetative, inflorescence, floral, and root growth, such that meristem fate defines the ability to persist past annual, and into biennial or perennial strategies. Perennial plants, by definition, must maintain at least one meristem past the first growing season and so allocate some, but not all, meristems to reproduction while preserving others for subsequent years. Thus, the shoot apical meristem of perennial plants remains indeterminate while the plant is in the vegetative stage [17]. In many perennial grass species, meristems are reserved or newly generated from the crown and thus facilitate tillering and regrowth following herbivory, stress damage, or seasonal dormancy [18]. One mechanism to maintain meristem indeterminacy is clonality, a vegetative reproduction strategy whereby genetically identical units emerging from the original plant spread as rhizomes or adventitious stems and continue to grow, thus preserving and extending meristems over space and time. This strategy is observed in some perennial species but is by no means universal and intraspecific variation in the capacity to produce rhizomes is often observed (e.g. [19, 20]).

<u>*Growth and its drivers*</u>

Annual and perennial plants differ in how they grow and allocate resources to specific tissues. A key concept here is relative growth rate (RGR) – the biomass added per unit time as a function of total plant biomass. RGR can be modelled as the product of specific leaf area (SLA), leaf mass ratio (LMR) and the net assimilation rate (NAR; see Table 1 for a discussion of these parameters) [21]. This perspective of RGR variation suggests that alterations in nearly all aspects of plant function – from whole plant partitioning (LMR) to leaf anatomy (SLA) and rates of primary metabolism (NAR) – could cause differences in growth rate.

The relative growth rate of perennial plants is generally slower than annuals during the first season of growth when corrected for phylogenetic similarity (Fig 2a) [22-25]. One large-scale experiment using phylogenetic comparative analyses to compare RGR of 382 grass species found that growth rate is most strongly associated with whether a grass used the annual or perennial strategy (see Supplemental Table 2 in [26]). Perennial species had less total leaf area on a whole-plant basis but LMR did not differ between annuals and perennials because perennials generally had denser leaves, or lower SLA (Fig 2c and 2e). An earlier study comparing six congeneric pairs of annual and perennial grass species also found consistently higher RGR in annuals and identified SLA and the rate of new leaf production as the driving factors in these differences [23].

Traditionally, it has been assumed that annuals allocate proportionally more fixed carbon toward reproduction than perennials each year [27], while greater investment in cold tolerance mechanisms (*e.g.,* via fructan accumulation; [28]) and larger root systems may compete with seed development for photosynthate in perennials. Several studies bear this out as related to competing investment in roots and seeds. The annual *Lupinus nanus* devotes over 60% of its energy toward reproduction and less than 5% to roots, while the perennial congener *L. variicolor* uses only 18% of its annual energy budget toward reproduction and over 40% to support its large taproot system [29]. Under fertile soils, the annual grass *Bromus madritensis* allocated approximately 37% of total annual net carbon assimilation toward root tissue, while the perennial congener *B. erectus* allocated nearly 50% of annual carbon assimilation toward roots [30].

Comprehensive surveys, however, find little support for the notion that perennials invest comparatively more photosynthate in roots than annuals. A study of 14 grass species representing six congeneric annual/perennial pairs found that the ratio of root to shoot mass did not differ between these two strategies, though roots of perennial species had higher dry to fresh mass ratios, suggesting the existence of anatomical differences in the roots of annual and perennial grasses [23]. The large dataset of 382 grasses, discussed above [26], found that root to shoot mass ratios differed between annual and perennial grasses early during development but that this difference was not seen in older grasses (Fig. 2d and f), suggesting that allocation patterns change over time. It should be noted, however, that these studies assessed growth in pots or hydroponic culture over a single, short simulated growing season; possible differences between annuals and perennials in longer-term patterns of root growth versus reproductive output have not been assessed. One important note in this regard is that estimating lifetime reproductive output is challenging and rarely attempted for perennial taxa. Long-term ecological experiments contrasting lifetime fitness of annuals and perennials are needed to make general statements about the relative investment in reproduction versus vegetative tissues.

Leaf anatomy

Leaf anatomy of annual and perennial plants differs in ways that may facilitate each strategy. For example, annual leaves enable greater carbon acquisition than perennials on a leaf area basis via higher SLA (Fig 2b), while perennial leaf structure promotes persistence and defense via higher tissue density and leaf thickness (*i.e.,* lower SLA; [23, 25, 31]). Many perennials achieve denser leaves than annuals by investing less in thin-walled mesophyll tissue and more in high-density epidermis, vascular, and schlerenchyma tissues, while holding less water than annual leaves [32, 33]. Perennial leaves can in some cases achieve greater vasculature area by enhanced vein density, not via larger vascular bundles, and, while they have smaller mesophyll cells than annual plants, leaves of both strategies have similar epidermal cell sizes and cuticle thicknesses [33, 34]. Collectively, these structural observations are consistent with a higher possible rate of carbon assimilation in annuals trading off with more persistent leaves in perennials.

Root anatomy

While general patterns of relative investment in above- and below-ground biomass are equivocal, perennial species generally differ from annuals in root traits related to nutrient uptake and longevity. For instance, annuals maximize below ground resource acquisition via greater specific root length, and root nitrogen concentration. Perennial plants, on the other hand, maximize resource conservation and root persistence via higher root tissue density, root diameter, and root dry weight [35-37]. The development of underground storage organs, such as rhizomes, stolons or tubers, can be important for perennial functionality as they allow vegetative propagation and facilitate persistence in challenging environments. In particular, the root systems of perennial species are better equipped to source water from the soil, buffering them from fluctuating water availability [38]. These storage organs permit some perennial species to achieve greater nutrient use efficiencies (NUE) via recycling mechanisms whereby nutrients accumulated in the leaves during growth are relocated to the roots during non-active phases, then later returned to the leaves for re-use during subsequent growth periods. This pattern of nutrient translocation has been documented in several perennial grass species in which translocation is a target of artificial selection to increase NUE in biofuel crops [39].

ECO-PHYSIOLOGY OF PERENNIALITY

Resource Use Efficiency

The efficiency with which plants can use resources, such as carbon, water, and nutrients, is a central determinant of a plant's ecology. Traditionally, perennial plants were believed to assimilate carbon at slower rates than annual species [32]. For instance, the net daily rate of leaf photosynthesis was over 50% greater in the annual domesticated *Hordeum vulgare* than the wild, slow growing perennial *H. bulbosum* [25]. However, a detailed study of physiology across 42 grass species found that the annual species had only slightly higher net rates of carbon assimilation than the perennials which, in combination with higher stomatal conductance, resulted in slightly lower water-use efficiency compared to the perennial grasses [40]. Moreover, this study also identified key traits that were influenced by both life history and photosynthesis type. For example, leaf hydraulic conductance -- the ability for water to flow throughout the plant -- was higher in annual grasses using C_4 photosynthesis compared to annual C_3 grasses, yet was similar across perennial grasses regardless of photosynthetic type [40]. Additional studies contrasting domesticated annual and perennial species likewise found limited support for the hypothesis that annuals have higher rates of carbon assimilation, noting that past artificial selection may have altered the balance between acquisition and allocation [41, 42]. These findings suggest that distinguishing differences in physiology between annual and perennial strategies is complex and that plants interactively exploit photosynthetic pathways and life history strategies to best adapt to a diversity of niches.

While comprehensive comparative data are scarce and metrics to assess NUE vary from study-to-study, perennial plants have been assumed to use nutrients more efficiently than annuals [9, 43, 44]. An analysis of annual and perennial *Physaria* species (Brassicaceae) found that the perennial species allocated more nitrogen to green tissue and achieved overall greater nitrogen use efficiency through reduced nitrogen loss from senescence and longer leaf life-spans as compared to annuals [45]. Field-level comparisons of mixed perennials and annual winter wheat found higher levels of soil N and C in the perennial fields [44]. Though frequently cited as evidence of higher NUE in perennials (e.g. [9]), these latter field-level measurements are statements about community-level processes; resolving whether and how individual species control NUE physiologically and developmentally is critical for efforts to understand evolutionary transitions and to develop perennial crop species.

Regulation of Source:Sink Dynamics

Plant physiologists distinguish between tissues that serve as a source for carbon, nutrients, or water versus those that serve as a sink for these resources. Photosynthetic tissues such as leaves and the stems of some species are the primary source for carbon, while roots are the source for nearly all other resources. All tissues begin as sink tissues, because the developmental cost of constructing them outpaces their initial capacity as sources, *e.g.* a leaf might begin as a sink for nitrogen and then become a source during senescence when nutrients are remobilized for seed development. The dynamic relationship between source and sink tissues is poorly understood at the whole-plant scale [46]. At the leaf level, the balance between carbon available for respiration, storage, or transport is regulated primarily via feedbacks on photosynthesis. Because proteins are themselves nitrogen sinks, the abundance and activity of enzymes involved in photosynthesis represent a tight coupling between nitrogen storage and carbon fixation. Carbon and or nutrients not needed for maintenance of source tissues are loaded into the phloem for use elsewhere in the plant, with their destination presumably driven by sink tissue strength.

How herbaceous perennials control nutrient resorption and reallocation at the end of a growing season is poorly understood, though many molecular components controlling related processes have been described in model annual plants [47]. Re-mobilization of nitrogen during leaf senescence requires proteins and pathways involved in autophagy and programmed cell death [48], as well as those that convert liberated nitrogen into compounds amenable to transportation into sink tissues [49]. Once released from leaves, most nitrogen is transported via the vascular system to developing seeds and/or storage tissues, such as stems and roots. While there is little direct evidence, the control of the sink strength in roots may be controlled by the activity of root-expressed amino acid synthetases [50]. Nitrogen sink strength in Arabidopsis seeds is controlled, in part, by seed-expressed amino acid and nitrate transporters [51].

How the relative sink strength of roots and seeds is controlled -- presumably a key difference between annual and perennial plants -- is currently unknown. One interesting observation here, is that the degree to which nitrogen that is loaded into developing seeds is remobilized from leaves versus directly taken up from soil varies substantially among plant species and environmental conditions [50]. For example, the proportion of nitrogen loaded into developing spikes arising from remobilized nitrogen at anthesis varied from 51 to 91% among cultivars of bread wheat [52]. Such diversity could facilitate functional analyses of source/sink dynamics among species with contrasting life history strategies. Carbon sink strength is driven, in part, by the activity of sucrose transporters which control phloem unloading in sink tissues [53]. Development likely also plays a role by regulating the physical sizes and growth rates of competing sink organs. Additional work is needed to decouple the contributions of physiological (*i.e.* via dynamic feedback between source and sink tissues, or between sink tissues) and developmental (*i.e.* via relative size differences between sink tissues) processes, and their possible role in evolutionary transitions between annual and perennial strategies. An analogous transition that may provide insight is the source/sink dynamics targeted during plant domestication, wherein artificial selection for increased investment in reproductive output often came at the expense of investment in defense or stem strength [54]. The control of sink strength in iteroparous vs semelparous annuals may also provide a good model for these processes [55].

GENETICS OF PERENNIALITY

One take-away from our discussion is that diverse aspects of plant development, metabolism, and physiology may differ between annual and perennial species. Conceptualizing perenniality as a multi-trait syndrome thus provides a framework to study the genetic control of each constituent trait as well as their genetic correlations. This also provides a framework to assess the role that natural selection plays in shaping life histories in natural populations and the prospects for breeding perennial crops. Critically, understanding the genetic basis of a trait allows us to determine the relative contributions of genetics and the environment to the expression of the trait. Some traits may be under strict genetic control, with little trait variation within species attributable to the effects of the environment. Plants may also have the ability to adjust traits in response to environmental cues; in many species, the transition from vegetative to reproductive growth is triggered by changes in light, temperature, or resource availability. Natural populations of plants may also harbour genetic variation in the extent to which a trait responds to environmental cues, or Genotype by Environment interaction, which represents heritable variation that natural selection or breeders may use to shape the plasticity of plants over generations [56]. Tools from quantitative genetics can disentangle these varying contributions of genotype and the environment [57].

Molecular control of phenology

The most detailed assessment of the genetic basis of an individual component of perenniality regards the control of meristem fate in *Arabis alpina,* a perennial relative of the annual model species *Arabidopsis thaliana*. The role of cold temperatures in regulating the transition from vegetative to reproductive development is exceptionally well-characterized in *A. thaliana* and, in large part, is mediated by the flowering repressor Flowering Locus C (FLC), which is transcriptionally silenced by extended cold temperature. In *Arabis alpina*, cold also represses the ortholog of FLC (AaPEP1) in a similar manner, but the transcriptional repression of AaPEP1 is transient such that any meristems arising after the cold treatment are again inhibited from flowering by functional AaPEP1 [58]. These repressed meristems are consequently reserved for subsequent seasons and will themselves require a cold period to become competent to flower.

Genetic basis of perennating structures

Genetic control of the development of perennating structures has been studied in the perennial relatives of several prominent annual crop species [59-61]. Interspecific crosses facilitate discovery of genetic loci controlling these and other traits that distinguish annuals and perennials. Crosses between cultivated annual *Zea mays* (which lacks rhizomes) and wild perennial *Z. diploperennis* (which develops numerous rhizomes) reveal two genetic loci that together explain 12% of phenotypic variance in the cross [60]. Differences between annual *Sorghum bicolor* (lacking rhizomes) and perennial *S. propinquum* (abundant rhizomes) in the number of rhizomes produced and the extent of their growth are likewise controlled by several genetic loci that explain little phenotypic variation in this trait [59]. These results suggest that differences in rhizome productivity in *Zea* and *Sorghum* are controlled by many additional undetected genetic loci of small effect and/or have a large environmental component to their expression. By contrast, interspecific crosses between the annual *Oryza sativa* and perennial *O. longistaminata* suggest fairly simple inheritance of rhizome production, with segregation ratios indicating two loci affecting the presence or absence of rhizomes [61]. Remarkably, these two loci apparently co-localize with the *Sorghum* rhizome QTL described above, suggesting either evolutionary convergence or conservation of the genetic control of rhizome formation. Disentangling the genetic and environmental controls (and their interactions) of components of the perennial syndrome such as rhizomatousness must be a priority when developing perennial crops.

Carbon and nutrients that are stored in the roots or shoots of perennial species are potentially available to facilitate regrowth in subsequent seasons. In *Sorghum*, the loci affecting differences in rhizome production co-localize with loci associated with re-growth [59]. Re-growth in perennial *Zea diploperennis* has a simple two locus inheritance, though the effects of additional genetic modifiers and/or environment on this trait cannot be excluded [19]. Genetic analyses of ratooning varieties of rice, from which multiple harvests are taken from a single planting in a growing season (*i.e.* iteroparity in an annual species; Fig. 1), have yielded several insights into re-growth where growing seasons are long. Because the first harvest removes biomass and nutrients, these plants must have sufficient reserves to initiate a second round of growth later that same season. Genetic loci associated with within-species variation in re-growth have been identified in rice [20]. Whether this capacity for re-growth in annual ratoon crops involves the same genetic and developmental mechanisms of re-growth seen in perennials is not currently known. However, if there is a common genetic basis between ratooning ability and re-growth in perennials then studying ratooning rice should help to identify the molecular mechanisms driving this key aspect of the perennial syndrome.

The molecular control of growth rate

New phenomic technologies allow for extremely precise, repeated measures of growth rate, including its response to environmental cues [62]. However, because of past empirical challenges with measuring and modelling growth rate accurately and the likely highly polygenic architecture of growth rate, little is presently known about the genetic or molecular control of growth rate, *per se*. Garnier [23] proposed that differences in growth rate – regardless of whether a plant is annual or perennial – may be a simple function of leaf anatomy and its relationship to the rate of photosynthesis and the generation of new leaf matter. If true, clarity on the molecular basis of RGR may be found through careful integrated study of leaf development and rates of carbon assimilation and respiration. Analysis in annuals such as *Arabidopsis thaliana* have identified many genetic loci of small effect driving heritable differences in growth rate, including significant cyto-nuclear interaction [63] and provocative evidence of genetic trade-offs between growth rate, allometric scaling, life span, and stress tolerance [64]. Applying modern phenomic techniques to screen for genetic variation in annual by perennial mapping populations should allow for rapid progress in identifying the genetic and environmental controls of growth rate as related to life history transitions.

EVOLUTION OF PERENNIALITY

Despite the complexity of the perennial and annual syndromes, evolutionary transitions between them are common among herbaceous plant lineages [65-67], indicating that shifts in the underlying components are readily achieved. In terms of directionality, annual species are generally derived from perennial ancestors, *i.e.* transitions from perennial to annual states are more common than the reverse [65-67]. Thomas *et al.* [17] and Garnier [23] both argue that fairly simple changes in plant growth and cell death could translate to distinct annual or perennial phenotypes. In Garnier's view [23] natural selection for increased seedling growth rate (*e.g.* in short season environments) favors variants that increase the resource acquisition strategy of leaves at the expense of defense and leaf longevity. We argue that subsequent changes in two essential features would then lead to distinct differences between annual and perennial strategies. The first is the relative allocation of carbon and nutrients to either maximize a single reproductive output (*i.e.* semelparous annuals) or to ensure that the plant can retain sufficient reserves for maintenance respiration following reproduction and then endure and recover from extended periods of dormancy (*i.e.* perennials). The second differentiating feature is retention in perennials of meristems capable of regrowth in a second season. Changes in myriad other traits in response to change in growth rate and exposure to seasonal extremes might also be selected for in nascent annuals, including reduced tolerance to abiotic stressors and to herbivory, reduced investment in perennating structures, and less robust stems and leaf sheaths (in grasses).

PROSPECTS AND INSPIRATION FOR PERENNIAL CROPS

The perennial syndrome has been proposed to offer many benefits for agriculture, including reduced soil disturbance and greater water- and nutrient- use efficiencies compared to the annual life history strategy [9]. Despite these and other clear benefits of perennial plants with regards to cropping, the majority of our key food crops and all cereal crops are annual [7]. (Prominent current perennial crops include sugar cane, cellulosic biofuels such as *Miscanthus* and Switchgrass, and many plants used as animal feed). For some of these species, shifting from perennial to annual life history strategies was an important step during domestication [68]. Indeed, components of the annual syndrome, such as high growth rate and reduced investment in defense, may be favorable during domestication due to the resulting greater harvest indices (mass of harvestable grain : total plant mass) compared to perennials [6]. Introducing the complete perennial syndrome into crops might consequently hinder harvest indices [69, 70] and so the specific agronomically desirable components of perenniality and annuality, and their potential trade-offs, should be given careful consideration.

Active programs to breed perennial rice, wheat, sorghum, maize, and oilseed crops have had varying degrees of success [10]. For most of these systems, the strategy involves crossing elite crop varieties to related species that possess desirable components of the perenniality syndrome. Several patterns emerge where genetic crosses have yielded stable, viable, offspring. First, with the goal of increasing the range of feasible cropping environments, perennial rice was bred by crossing cultivated annual *Oryza sativa* with its perennial relative *O. longistaminata* [71] and targeting the introgression of alleles for rhizome expression into *O. sativa*. Researchers successfully generated a rice variety that produces stable yield over four growing seasons comparable to its annual parent [72], provided that field conditions were sufficiently mesic [73] and thereby highlighting the importance of understanding genotype by environment interactions in assessing trade-offs [56]. Perennial wheat was generated via crosses between domesticated annual wheat and several perennial Wheatgrasses (*Thynopyrum* spp.) [74]. However, in most of these successful genetic crosses, plot-level yields declined with each year of field trials owing to mortality of individual plants and reduced vigor in later seasons [74].

Our discussion of perenniality as a syndrome highlights the value of assessing the genetic correlations of its individual components during the design of breeding programs. We propose that crop improvement efforts should focus on engineering into annual species only the specific components of the perennial syndrome that convey higher quality yield, enhanced resource utilization or reduced environmental impact [10, 75]. The case of perennial rice breeding, which focused on introgressing rhizomatous re-growth into an annual crop, illustrates this approach. For the targeted approach to work in additional systems, a better understanding of the genetic architecture of individual components of perenniality is needed. (Rice, as a predominantly tropical and sub-tropical crop, may also not serve as a good model for temperate cereal crops in which overwintering will be essential.) Understanding the extent to which the components of perenniality are genetically correlated with one another and are physiologically or developmentally integrated is particularly important; independent assortment of constituent traits facilitates recombining subsets of traits into common genetic backgrounds.

Another research priority should be to assess whether existing breeding populations of our elite annual crops harbor genetic variation in individual components of the perennial syndrome and, if not, to identify wild relatives that may harbor such variation. This could be accomplished by identifying differences in, *e.g.* stress tolerance, nutrient resorption, leaf architecture, and RGR and its drivers (SLA, LMR and NAR) between the annual crop and closely related perennial species. Once key trait differences have been identified, along with their possible genetic correlations, these traits or their proxies could be screened among germplasm of annual crops to inform breeding targets. If the molecular control of such traits is identified in perennials, biotechnology could facilitate rapid deployment in elite annual germplasm via transgenic integration or CRISPR-mediated alteration of native genes [76]. A clearer understanding of essential differences between annual crops and perennial relatives could also facilitate improvement of perennials themselves by targeting domestication traits [77]. Biotechnology-driven approaches might be particularly attractive for systems where genetic crosses are challenging (e.g. due to differences in ploidy). A mechanistic understanding of the components of perenniality and their functional relationships may also pay dividends through improving resilience of existing annual crop species (grown as annuals) to environmental stress.

CONCLUSION

Millions of years of plant evolution generated a bewildering array of plant form and function, optimized for fitness in complex ecological settings. The components of these resulting strategies were subsequently exploited and manipulated by artificial selection to provide humanity with highly productive cropping systems. In many natural systems, life history strategies will be critical determinants of success under a rapidly changing global climate. Our current understanding of the mechanisms of plant-environment interactions and of how they can be best manipulated is woefully incomplete if we are to address existential challenges in managing ecosystems and expanding agricultural production. Careful, deliberate integration of physiological, developmental, and physiological research in well-chosen model and crop systems – along with collaboration between breeders, resource managers, and plant scientists – is essential to meet this challenge.

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BOX 1: KEY CONCEPTS IN PLANT LIFE HISTORY

Life History – The strategy employed by an organism to schedule developmental transitions and relative investment of resources to maximize fitness. Classically, life history strategy comprises an organism's size at birth (or the size of a seed), the rate and pattern (e.g. allocation to different organs) of growth, the timing of transitions to reproductive age and the duration of time spent reproducing, the number, quality, and sex of offspring, the timing of senescence, and the total lifespan.

Annual – A plant which completes its life cycle in a single growing season. Annuals plants may be iteroparous or semelparous (see below).

Perennial — A plant which persists over multiple growing seasons. Perennial plants may be iteroparous (e.g. many grass species) or semelparous (e.g. Agave "century plants").

Biennial – A plant which germinates and reproduces over two sequential growing seasons. Often winter cold, or vernalization, serves as a trigger to stimulate competency to flower during the second season.

Phenology – The pattern of developmental transitions during an organism's life, often cued by environmental factors. For plants, critical phenological transitions include germination, the transition to flowering, senescence and, for biennial or perennial plants, emergence of budburst during successive growing seasons.

Iteroparous – Condition wherein an organism reproduces multiple times during its life.

Semelparous – Condition wherein an organism reproduces only once.

Relative growth rate – The growth rate of a plant expressed as a function of its current biomass. Typically expressed as grams of new biomass per day per gram of total plant biomass (g g^{-1} d^{-1}). RGR is often modelled as the product of SLA, LMR, and NAR (see below).

SLA — Specific Leaf Area. The ratio of leaf area to mass. Typically expressed as grams of dry leaf mass per square leaf area (g cm^{-1}).

NAR– Net Assimilation Rate. The amount of biomass acquired per day as a function of leaf area (g cm^{-2} d^{-1}). NAR is a complex parameter that is driven by the rate of carbon assimilation and the rate of whole plant respiration. It may be strongly affected by the relative sizes -- and thus respiratory demands -- of leaves, stems, and roots.

LMR — Leaf Mass Ratio. The proportion of total plant dry biomass, including roots, that is comprised of leaves. Typically expressed as g g^{-1}.

Senescence – On a whole-plant basis this refers to the decrease in reproductive effort and increasing probability of mortality as life progresses. Individual leaves may also senesce, both according to age of the leaf and/or the effects of the environment.

Meristem – Specific regions of ongoing cell division which facilitate growth and the development of new organs.

FIGURES

Figure 1. Continuum of growth strategies. Schematic showing general timings of germination (GM), vegetative growth (VG), reproductive growth (RG), and senescence (S) and death (D) in

annual, biennial, triennial, and perennial strategies, distinguishing iteroparous from semelparous reproductive efforts.

Figure 2. Growth patterning in annual and perennial grasses. (A) RGR, relative growth rate; (B) SLA, specific leaf area; (C) LAR, leaf area ratio; (D) RMR, root mass ratio at the 20th percentile of growth; (E) LMR, leaf mass ratio, and (F) RMR, root mass ratio at the 60th percentile of growth in 115 annual (red) and 200 perennial (blue) grass species. Colored vertical lines indicate the means for each density plot. Data from [26]. Panels A-C, E-F show 60th percentile of growth data. Phylogenetic least squares regressions analyses, using the PGLS package [78] in R, were used to test for effects of life history group (annual, perennial).

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