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

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14 **ABSTRACT**

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

35 **KEYWORDS**

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

## 37 **INTRODUCTION**

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

53       Plants vary considerably in their relative resource allocation to growth, reproduction,  
54 defense, and storage with two extremes: *annual species*, which tend to reproduce once and then  
55 die, and *perennial species*, which delay reproduction past the first season or reproduce over  
56 multiple seasons, often with interim periods of quiescence. The majority of calories consumed by  
57 humans, both directly or via grain-fed animals, begin as photosynthate captured by annual plants  
58 including maize, wheat, soy, and rice [7]. Most molecular and physiological studies likewise  
59 employ annuals (e.g. [8]). In recent years, the prospect of developing perennial crops has

60 received attention as a means to reduce agricultural inputs, maintain soil health, and increase  
61 diversity in cropping systems [9]. There are now active programs aiming to breed perennial  
62 wheat, rice, sunflower, maize, and sorghum, among others [10]. The motivation for developing  
63 perennial cropping systems arises from the observation that, as compared to annual relatives,  
64 perennial species may be more stress-tolerant and resource-use efficient and may promote soil  
65 health via reduced mechanical tilling [9]. (We here focus on herbaceous plant species; the  
66 overwhelming majority of woody species are, of course, perennial, as well.) More generally,  
67 trade-offs in resource allocation are central to nearly all aspects of fundamental and applied plant  
68 science [11]. As one example, nutrients used to mount a constitutive defense against herbivores  
69 cannot be used for reproduction, thus reducing fitness in natural settings and yield in agriculture  
70 settings in the absence of such stressors.

71         In spite of the growing interest in developing perennial cropping systems, little recent  
72 research has been directed towards understanding the fundamental genetic, physiological and  
73 developmental differences, if any, between herbaceous annual and perennial species. Here, we  
74 use plant life history variation along an axis from annual to perennial habit as a means to explore  
75 trade-offs in resource allocation and consider these trade-offs in the context of the evolution of  
76 life histories as well as the prospects for perennial crop breeding. We first identify the  
77 components of perennial *versus* annual strategies and evaluate classic assumptions about  
78 differences between the two types in their growth, anatomy, rates of resource acquisition, and  
79 relative investment in source and sink organs. Throughout, we present the case that perenniality,  
80 annuality, and intermediate forms are *syndromes* comprised of many traits. We assess the extent  
81 to which constituent traits are functionally integrated and ask whether they are under genetically  
82 independent control. While some breeding programs target perenniality *per se* as a breeding

83 goal, we present the case that life history syndromes likely evolved on a trait-by-trait basis and  
84 we argue that breeding for only specific components of perenniality may prove more fruitful in  
85 the long term. Specifically, by assessing the physiological integration and genetic segregation  
86 patterns of individual life history traits, breeders might select desirable combinations of both  
87 “annual” and “perennial” traits.

88

## 89 ***WHAT ARE THE UNDERLYING COMPONENTS OF PERENNIALITY?***

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### 90 *Phenology*

91 There exists a broad diversity of phenological patterns within herbaceous perennial taxa (Fig 1).  
92 For example, some species persist in a non-reproductive vegetative stage year-round and may have  
93 multiple flowering periods per year, as is often observed in wet-tropic perennials. Other perennial  
94 herbs common to environments with pronounced seasons have a single reproductive phase per  
95 year. In these latter species, the above ground tissues tend to die back annually with winter frost  
96 or summer heat and aridity, while the below ground crown and root system persist to facilitate  
97 resprouting [12]. The environment, in general, plays an important role in the phenology of plants.  
98 For example, compelling evidence links precipitation to phenological shifts in Mojave Desert  
99 ecosystems where, despite their unpredictable timing and intensity, autumn rain events clearly  
100 trigger mass germination of annuals and also vegetative growth and consequently spring  
101 reproductive growth in perennials [13]. Light intensity may also influence phenology as when, for  
102 example, the perennial herb *Senecio integrifolius* flowers earlier when exposed to full sun as  
103 compared to conspecifics growing under shade [14]. Finally, temperature influences phenology,  
104 as many species require exposure to cold (*i.e.*, vernalization) or accumulated days of warmth to  
105 germinate or transition to reproduction [15]. These relationships between phenology and

106 environment suggest that the environment triggers shifts in life stage. However the degrees to  
107 which environment *versus* genetics contribute toward phenology is not well known in perennials  
108 and, indeed, is understood for only a few annuals and biennials [16].

109

### 110 Meristem determinacy

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

124

### 125 Growth and its drivers

126 Annual and perennial plants differ in how they grow and allocate resources to specific tissues. A  
127 key concept here is relative growth rate (RGR) – the biomass added per unit time as a function of  
128 total plant biomass. RGR can be modelled as the product of specific leaf area (SLA), leaf mass

129 ratio (LMR) and the net assimilation rate (NAR; see Table 1 for a discussion of these parameters)  
130 [21]. This perspective of RGR variation suggests that alterations in nearly all aspects of plant  
131 function – from whole plant partitioning (LMR) to leaf anatomy (SLA) and rates of primary  
132 metabolism (NAR) – could cause differences in growth rate.

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

142         Traditionally, it has been assumed that annuals allocate proportionally more fixed carbon  
143 toward reproduction than perennials each year [27], while greater investment in cold tolerance  
144 mechanisms (*e.g.*, via fructan accumulation; [28]) and larger root systems may compete with seed  
145 development for photosynthate in perennials. Several studies bear this out as related to competing  
146 investment in roots and seeds. The annual *Lupinus nanus* devotes over 60% of its energy toward  
147 reproduction and less than 5% to roots, while the perennial congener *L. variicolor* uses only 18%  
148 of its annual energy budget toward reproduction and over 40% to support its large taproot system  
149 [29]. Under fertile soils, the annual grass *Bromus madritensis* allocated approximately 37% of total  
150 annual net carbon assimilation toward root tissue, while the perennial congener *B. erectus* allocated  
151 nearly 50% of annual carbon assimilation toward roots [30].

152           Comprehensive surveys, however, find little support for the notion that perennials invest  
153 comparatively more photosynthate in roots than annuals. A study of 14 grass species representing  
154 six congeneric annual/perennial pairs found that the ratio of root to shoot mass did not differ  
155 between these two strategies, though roots of perennial species had higher dry to fresh mass ratios,  
156 suggesting the existence of anatomical differences in the roots of annual and perennial grasses  
157 [23]. The large dataset of 382 grasses, discussed above [26], found that root to shoot mass  
158 ratios differed between annual and perennial grasses early during development but that this  
159 difference was not seen in older grasses (Fig. 2d and f), suggesting that allocation patterns change  
160 over time. It should be noted, however, that these studies assessed growth in pots or hydroponic  
161 culture over a single, short simulated growing season; possible differences between annuals and  
162 perennials in longer-term patterns of root growth versus reproductive output have not been  
163 assessed. One important note in this regard is that estimating lifetime reproductive output is  
164 challenging and rarely attempted for perennial taxa. Long-term ecological experiments contrasting  
165 lifetime fitness of annuals and perennials are needed to make general statements about the relative  
166 investment in reproduction versus vegetative tissues.

167

### 168 Leaf anatomy

169 Leaf anatomy of annual and perennial plants differs in ways that may facilitate each strategy. For  
170 example, annual leaves enable greater carbon acquisition than perennials on a leaf area basis via  
171 higher SLA (Fig 2b), while perennial leaf structure promotes persistence and defense via higher  
172 tissue density and leaf thickness (*i.e.*, lower SLA; [23, 25, 31]). Many perennials achieve denser  
173 leaves than annuals by investing less in thin-walled mesophyll tissue and more in high-density  
174 epidermis, vascular, and sclerenchyma tissues, while holding less water than annual leaves [32,

175 33]. Perennial leaves can in some cases achieve greater vasculature area by enhanced vein density,  
176 not via larger vascular bundles, and, while they have smaller mesophyll cells than annual plants,  
177 leaves of both strategies have similar epidermal cell sizes and cuticle thicknesses [33, 34].  
178 Collectively, these structural observations are consistent with a higher possible rate of carbon  
179 assimilation in annuals trading off with more persistent leaves in perennials.

180

### 181 Root anatomy

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

197

199 *Resource Use Efficiency*

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200 The efficiency with which plants can use resources, such as carbon, water, and nutrients, is a  
201 central determinant of a plant's ecology. Traditionally, perennial plants were believed to assimilate  
202 carbon at slower rates than annual species [32]. For instance, the net daily rate of leaf  
203 photosynthesis was over 50% greater in the annual domesticated *Hordeum vulgare* than the wild,  
204 slow growing perennial *H. bulbosum* [25]. However, a detailed study of physiology across 42 grass  
205 species found that the annual species had only slightly higher net rates of carbon assimilation than  
206 the perennials which, in combination with higher stomatal conductance, resulted in slightly lower  
207 water-use efficiency compared to the perennial grasses [40]. Moreover, this study also identified  
208 key traits that were influenced by both life history and photosynthesis type. For example, leaf  
209 hydraulic conductance -- the ability for water to flow throughout the plant -- was higher in annual  
210 grasses using C<sub>4</sub> photosynthesis compared to annual C<sub>3</sub> grasses, yet was similar across perennial  
211 grasses regardless of photosynthetic type [40]. Additional studies contrasting domesticated annual  
212 and perennial species likewise found limited support for the hypothesis that annuals have higher  
213 rates of carbon assimilation, noting that past artificial selection may have altered the balance  
214 between acquisition and allocation [41, 42]. These findings suggest that distinguishing differences  
215 in physiology between annual and perennial strategies is complex and that plants interactively  
216 exploit photosynthetic pathways and life history strategies to best adapt to a diversity of niches.

217

218 While comprehensive comparative data are scarce and metrics to assess NUE vary from study-to-  
219 study, perennial plants have been assumed to use nutrients more efficiently than annuals [9, 43,  
220 44]. An analysis of annual and perennial *Physaria* species (Brassicaceae) found that the perennial

221 species allocated more nitrogen to green tissue and achieved overall greater nitrogen use efficiency  
222 through reduced nitrogen loss from senescence and longer leaf life-spans as compared to annuals  
223 [45]. Field-level comparisons of mixed perennials and annual winter wheat found higher levels of  
224 soil N and C in the perennial fields [44]. Though frequently cited as evidence of higher NUE in  
225 perennials (e.g. [9]), these latter field-level measurements are statements about community-level  
226 processes; resolving whether and how individual species control NUE physiologically and  
227 developmentally is critical for efforts to understand evolutionary transitions and to develop  
228 perennial crop species.

229

### 230 *Regulation of Source:Sink Dynamics*

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

244

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

255

256 How the relative sink strength of roots and seeds is controlled -- presumably a key difference  
257 between annual and perennial plants -- is currently unknown. One interesting observation here, is  
258 that the degree to which nitrogen that is loaded into developing seeds is remobilized from leaves  
259 versus directly taken up from soil varies substantially among plant species and environmental  
260 conditions [50]. For example, the proportion of nitrogen loaded into developing spikes arising  
261 from remobilized nitrogen at anthesis varied from 51 to 91% among cultivars of bread wheat [52].  
262 Such diversity could facilitate functional analyses of source/sink dynamics among species with  
263 contrasting life history strategies. Carbon sink strength is driven, in part, by the activity of sucrose  
264 transporters which control phloem unloading in sink tissues [53]. Development likely also plays a  
265 role by regulating the physical sizes and growth rates of competing sink organs. Additional work  
266 is needed to decouple the contributions of physiological (*i.e.* via dynamic feedback between source

267 and sink tissues, or between sink tissues) and developmental (*i.e.* via relative size differences  
268 between sink tissues) processes, and their possible role in evolutionary transitions between annual  
269 and perennial strategies. An analogous transition that may provide insight is the source/sink  
270 dynamics targeted during plant domestication, wherein artificial selection for increased investment  
271 in reproductive output often came at the expense of investment in defense or stem strength [54].  
272 The control of sink strength in iteroparous vs semelparous annuals may also provide a good model  
273 for these processes [55].

274

### 275 ***GENETICS OF PERENNIALITY***

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276 One take-away from our discussion is that diverse aspects of plant development, metabolism, and  
277 physiology may differ between annual and perennial species. Conceptualizing perennality as a  
278 multi-trait syndrome thus provides a framework to study the genetic control of each constituent  
279 trait as well as their genetic correlations. This also provides a framework to assess the role that  
280 natural selection plays in shaping life histories in natural populations and the prospects for  
281 breeding perennial crops. Critically, understanding the genetic basis of a trait allows us to  
282 determine the relative contributions of genetics and the environment to the expression of the trait.  
283 Some traits may be under strict genetic control, with little trait variation within species attributable  
284 to the effects of the environment. Plants may also have the ability to adjust traits in response to  
285 environmental cues; in many species, the transition from vegetative to reproductive growth is  
286 triggered by changes in light, temperature, or resource availability. Natural populations of plants  
287 may also harbour genetic variation in the extent to which a trait responds to environmental cues,  
288 or Genotype by Environment interaction, which represents heritable variation that natural selection

289 or breeders may use to shape the plasticity of plants over generations [56]. Tools from quantitative  
290 genetics can disentangle these varying contributions of genotype and the environment [57].

291

### 292 *Molecular control of phenology*

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

303

### 304 *Genetic basis of perennating structures*

305 Genetic control of the development of perennating structures has been studied in the perennial  
306 relatives of several prominent annual crop species [59-61]. Interspecific crosses facilitate  
307 discovery of genetic loci controlling these and other traits that distinguish annuals and perennials.  
308 Crosses between cultivated annual *Zea mays* (which lacks rhizomes) and wild perennial *Z.*  
309 *diploperennis* (which develops numerous rhizomes) reveal two genetic loci that together explain  
310 12% of phenotypic variance in the cross [60]. Differences between annual *Sorghum bicolor*  
311 (lacking rhizomes) and perennial *S. propinquum* (abundant rhizomes) in the number of rhizomes

312 produced and the extent of their growth are likewise controlled by several genetic loci that explain  
313 little phenotypic variation in this trait [59]. These results suggest that differences in rhizome  
314 productivity in *Zea* and *Sorghum* are controlled by many additional undetected genetic loci of  
315 small effect and/or have a large environmental component to their expression. By contrast,  
316 interspecific crosses between the annual *Oryza sativa* and perennial *O. longistaminata* suggest  
317 fairly simple inheritance of rhizome production, with segregation ratios indicating two loci  
318 affecting the presence or absence of rhizomes [61]. Remarkably, these two loci apparently co-  
319 localize with the *Sorghum* rhizome QTL described above, suggesting either evolutionary  
320 convergence or conservation of the genetic control of rhizome formation. Disentangling the  
321 genetic and environmental controls (and their interactions) of components of the perennial  
322 syndrome such as rhizomatousness must be a priority when developing perennial crops.

323

324 Carbon and nutrients that are stored in the roots or shoots of perennial species are potentially  
325 available to facilitate regrowth in subsequent seasons. In *Sorghum*, the loci affecting differences  
326 in rhizome production co-localize with loci associated with re-growth [59]. Re-growth in perennial  
327 *Zea diploperennis* has a simple two locus inheritance, though the effects of additional genetic  
328 modifiers and/or environment on this trait cannot be excluded [19]. Genetic analyses of ratooning  
329 varieties of rice, from which multiple harvests are taken from a single planting in a growing season  
330 (*i.e.* iteroparity in an annual species; Fig. 1), have yielded several insights into re-growth where  
331 growing seasons are long. Because the first harvest removes biomass and nutrients, these plants  
332 must have sufficient reserves to initiate a second round of growth later that same season. Genetic  
333 loci associated with within-species variation in re-growth have been identified in rice [20].  
334 Whether this capacity for re-growth in annual ratoon crops involves the same genetic and

335 developmental mechanisms of re-growth seen in perennials is not currently known. However, if  
336 there is a common genetic basis between ratooning ability and re-growth in perennials then  
337 studying ratooning rice should help to identify the molecular mechanisms driving this key aspect  
338 of the perennial syndrome.

339

#### 340 *The molecular control of growth rate*

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

356

#### 357 ***EVOLUTION OF PERENNIALITY***

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

376

## 377 **PROSPECTS AND INSPIRATION FOR PERENNIAL CROPS**

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378 The perennial syndrome has been proposed to offer many benefits for agriculture, including  
379 reduced soil disturbance and greater water- and nutrient- use efficiencies compared to the annual  
380 life history strategy [9]. Despite these and other clear benefits of perennial plants with regards to

381 cropping, the majority of our key food crops and all cereal crops are annual [7]. (Prominent current  
382 perennial crops include sugar cane, cellulosic biofuels such as *Miscanthus* and Switchgrass, and  
383 many plants used as animal feed). For some of these species, shifting from perennial to annual life  
384 history strategies was an important step during domestication [68]. Indeed, components of the  
385 annual syndrome, such as high growth rate and reduced investment in defense, may be favorable  
386 during domestication due to the resulting greater harvest indices (mass of harvestable grain : total  
387 plant mass) compared to perennials [6]. Introducing the complete perennial syndrome into crops  
388 might consequently hinder harvest indices [69, 70] and so the specific agronomically desirable  
389 components of perenniality and annuality, and their potential trade-offs, should be given careful  
390 consideration.

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

403 these successful genetic crosses, plot-level yields declined with each year of field trials owing to  
404 mortality of individual plants and reduced vigor in later seasons [74].

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

418 Another research priority should be to assess whether existing breeding populations of our  
419 elite annual crops harbor genetic variation in individual components of the perennial syndrome  
420 and, if not, to identify wild relatives that may harbor such variation. This could be accomplished  
421 by identifying differences in, *e.g.* stress tolerance, nutrient resorption, leaf architecture, and RGR  
422 and its drivers (SLA, LMR and NAR) between the annual crop and closely related perennial  
423 species. Once key trait differences have been identified, along with their possible genetic  
424 correlations, these traits or their proxies could be screened among germplasm of annual crops to  
425 inform breeding targets. If the molecular control of such traits is identified in perennials,

426 biotechnology could facilitate rapid deployment in elite annual germplasm via transgenic  
427 integration or CRISPR-mediated alteration of native genes [76]. A clearer understanding of  
428 essential differences between annual crops and perennial relatives could also facilitate  
429 improvement of perennials themselves by targeting domestication traits [77]. Biotechnology-  
430 driven approaches might be particularly attractive for systems where genetic crosses are  
431 challenging (e.g. due to differences in ploidy). A mechanistic understanding of the components of  
432 perenniality and their functional relationships may also pay dividends through improving  
433 resilience of existing annual crop species (grown as annuals) to environmental stress.

434

## 435 **CONCLUSION**

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

446

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452

### 453 **BOX 1: KEY CONCEPTS IN PLANT LIFE HISTORY**

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

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

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

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

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

471 Iteroparous – Condition wherein an organism reproduces multiple times during its life.  
472 Semelparous – Condition wherein an organism reproduces only once.  
473 Relative growth rate – The growth rate of a plant expressed as a function of its current biomass.  
474 Typically expressed as grams of new biomass per day per gram of total plant biomass ( $\text{g g}^{-1}$   
475  $\text{d}^{-1}$ ). RGR is often modelled as the product of SLA, LMR, and NAR (see below).  
476 SLA — Specific Leaf Area. The ratio of leaf area to mass. Typically expressed as grams of dry  
477 leaf mass per square leaf area ( $\text{g cm}^{-1}$ ).  
478 NAR— Net Assimilation Rate. The amount of biomass acquired per day as a function of leaf area  
479 ( $\text{g cm}^{-2} \text{d}^{-1}$ ). NAR is a complex parameter that is driven by the rate of carbon assimilation  
480 and the rate of whole plant respiration. It may be strongly affected by the relative sizes --  
481 and thus respiratory demands -- of leaves, stems, and roots.  
482 LMR — Leaf Mass Ratio. The proportion of total plant dry biomass, including roots, that is  
483 comprised of leaves. Typically expressed as  $\text{g g}^{-1}$ .  
484 Senescence – On a whole-plant basis this refers to the decrease in reproductive effort and  
485 increasing probability of mortality as life progresses. Individual leaves may also senesce,  
486 both according to age of the leaf and/or the effects of the environment.  
487 Meristem – Specific regions of ongoing cell division which facilitate growth and the development  
488 of new organs.

489

## 490 **FIGURES**

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

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

495

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

503

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