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The Evolution of Annual and Perennial Plant Life Histories: Ecological Correlates and Genetic Mechanisms

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Abstract

Flowering plants exhibit two principal life-history strategies: annuality (living and reproducing in one year) and perenniality (living more than one year). The advantages of either strategy depend on the relative benefits of immediate reproduction balanced against survivorship and future reproduction. This trade-off means that life-history strategies are associated with particular environments, with annuals being found more often in unpredictable habitats. Annuality and perenniality are the outcome of developmental genetic programs responding to their environment, with perennials being distinguished by their delayed competence to flower and reversion to growth after flowering. Evolutionary transitions between these strategies are frequent and have consequences for mating systems and genome evolution, with perennials being more likely to outcross with higher inbreeding depression and lower rates of molecular evolution. Integrating expectations from life-history theory with knowledge of the developmental genetics of flowering and seasonality is required to understand the mechanisms involved in the evolution of annual and perennial life histories.

1. INTRODUCTION

Meristem: a region of cells capable of ongoing cell division that gives rise to new tissues and organs

Determinate growth: the termination of growth once a structure has completely formed

The remarkable variation in life-history strategies among species reflects a diversity of solutions to the fundamental problem of optimizing reproduction and survival. In many taxa, the allocation and distribution of resources to reproduction within seasons versus between seasons can be astonishingly variable. In angiosperms, life spans can range from a few weeks in desert annuals like *Boerhavia* to over a thousand years in long-lived trees like baobabs (*Adansonia*). The diversity in plant life histories has made classification challenging and has led to various systems, for example, Raunkiær's (1934) classification of plant life forms based on morphology and the position of meristems at the end of the growing season. More widely used systems involve seasonal life expectancy (e.g., annual, biennial, perennial), or the number of reproductive bouts during life (monocarpy/semelparity, polycarpy/iteroparity). Arguments have been made for the utility of different classification systems (e.g., Kirkendall & Stenseth 1985, Silvertown 1989, Hughes 2017), but in large part the choice depends on the question of interest.

The continuum for life expectancy (with annuals at one end and perennials at the other) describes the distribution of reproductive effort among seasons, and life expectancy is often related, but not equivalent, to the number of reproductive bouts (on an axis that ranges from semelparity to iteroparity) (**Figure 1**). Annual plants can be divided into two types: (*a*) those that are truly semelparous with determinate growth (i.e., they reproduce once and die; this term is equivalent to the botanical term monocarpic) and concentrate their reproduction into a single episode where the main shoot apical meristem is used in the formation of a determinate inflorescence, and flowering

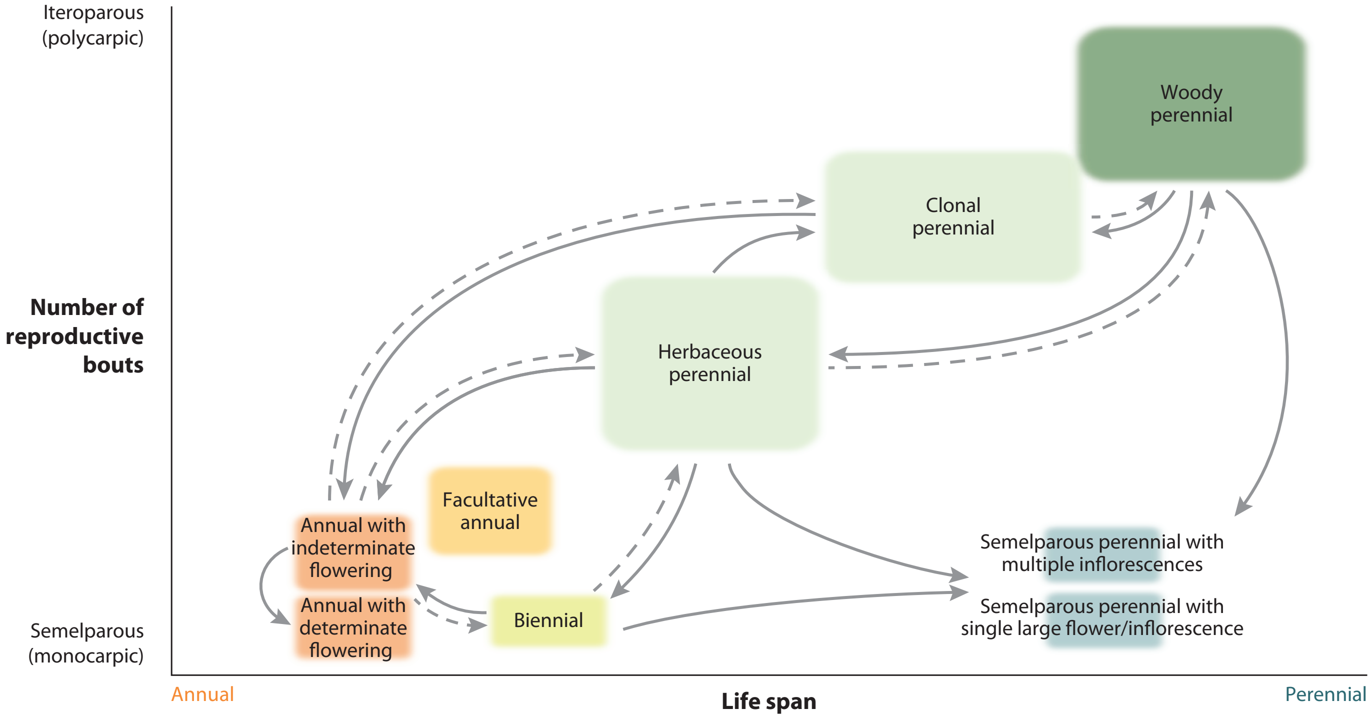

Figure 1

A diagrammatic representation of plant life history diversity. There are no natural breaks in the continuum of life cycles; separation into the categories of annual, perennial, semelparous, and iteroparous is somewhat arbitrary. Nonetheless, certain combinations are more common than others, and there are distinctive features of plants in the different categories. Solid lines with arrows indicate the most common order of evolutionary transitions between strategies, and dashed lines indicate when transitions are known to go in the other direction.

and seed set effectively end their life cycle, and (*b*) those with indeterminate growth that continue flowering until a climatic event ends their life (e.g., frost or drought). Biennials are plants that remain vegetative the first year, reproduce the second year, and then die. Biennials are relatively rare in the angiosperms, and their selective advantage is unclear (Silvertown 1986, and references therein). Perennial plants live for many years and most perennials are iteroparous (equivalent to the botanical term polycarpic), cycling back and forth between growth and reproduction and reproducing over multiple seasons. Not surprisingly, there exists considerable variation in the life span of different perennial species and when they initiate reproduction. Some perennials will flower in their first year (many herbaceous perennials), whereas others (many trees) have an extended juvenile phase before they start reproducing. In some species, perenniality is achieved through clonal reproduction (e.g., production of stolons or rhizomes) giving rise to new ramets so that the entire genet may be near immortal. Some perennials are semelparous; for example, species in at least 20 families grow for multiple years before a single massive and fatal reproductive event occurs (reviewed in Young & Augspurger 1991). Ultimately, life history diversity is the outcome of genetic programs of growth and development responding to environmental variation. These complex interactions mean that life histories are seldom unequivocal or categorical.

Indeterminate growth: growth that is not terminated and is facilitated by the production of meristems

Clonal reproduction: asexual reproduction through the propagation of plant parts not involving seeds

Life-history phenomena raise several related questions concerned with how natural selection shapes survivorship and reproduction as functions of age. Cole (1954) first pointed out that the persistence of iteroparity is paradoxical because a semelparous annual organism need only increase its average offspring size by one individual to achieve equivalent reproductive success to an iteroparous perennial. Why then would perenniality persist and evolve given the costly and unpredictable nature of surviving from one reproductive episode to the next? Cole's (1954) paper is often considered the starting point for a long tradition of formal, theoretical treatments on life-history evolution. The resolution of the paradox is largely credited to Charnov & Schaffer (1973) for recognizing that fecundity and survival are age specific, and their simple model can reveal the situations that benefit an annual over a perennial. The rate of population growth (λ) in an annual, a, is given by the product of survival from seed to flowering (C) and mean seed production (B_a):

$$\lambda_a = CB_a.$$

The equivalent expression for a perennial, p, includes adult survival (P):

$$\lambda_p = CB_p + P.$$

Then for an annual and perennial to have the same population growth rate ($\lambda_a = \lambda_p$), we obtain

$$B_a = B_p + \left(\frac{P}{C}\right).$$

It is evident that the advantage of one life history over the other depends on the ratio of adult to juvenile survival (i.e., P/C). The model predicts that perennials will be favored in environments where juvenile survival is low or unpredictable, and annuals will be favored when juvenile survival is high, and adult survival is low. This basic model has been elaborated to incorporate environmental stochasticity, the effects of density-dependent mortality, age structure, stage structure, and the extent of phenotypic plasticity (reviewed in Stearns 1992). While a review of the body of theory is beyond the scope of this article, consistent across models is the fact that the variation in juvenile versus adult survival largely depends on environment predictability.

Although substantial progress has been made in developing and empirically testing life-history theory, connecting this theory to the physiological and genetic mechanisms underlying reproductive decisions has proceeded more slowly. Recent interest in developing perennial crops and better understanding domesticated trees has led to a surge of interest in the physiology, evolution, and genetics of perennial species (Miller & Gross 2011, Lundgren & Des Marais 2020). In plants, the molecular and genetic mechanisms of reproduction, particularly flowering, have been well characterized in annual model systems such as *Arabidopsis thaliana* and various crop species. However, this in-depth characterization of flowering is seldom connected to the rich history of ecological research on reproductive effort and life-history decisions, nor to larger macroevolutionary trends on the frequency and direction of evolutionary transitions and the accompanying correlated traits. The lack of integration between fields has limited our ability to understand or predict evolutionary transitions between strategies and their adaptive significance.

Here, I provide a synthetic overview of the evolution of annual and perennial strategies in angiosperms. I focus the discussion on semelparous annual and iteroparous perennial plants because these are the most common strategies. Annual and perennial plants, as groups, share various ecological, reproductive, and genetic similarities, suggesting that the distribution of reproductive effort within versus between seasons has important evolutionary consequences. First, I illustrate important components of trade-offs between vegetative growth and reproduction and how these may evolve and affect plant fitness. Next, I consider the genetic mechanisms underlying differences in key traits that distinguish annuals and perennials. Then, I consider the direction and frequency of transitions between annual and perennial strategies in angiosperms. Finally, I identify some evolutionary consequences of different life histories, including key differences in mating and sexual systems and the ramifications of different life spans for genome evolution. I conclude by providing a research agenda for future work on annual and perennial life histories.

2. TRADE-OFFS BETWEEN REPRODUCTION AND GROWTH

The concept of trade-offs and differential allocation of limiting resources to reproduction versus growth and maintenance for survival is central to life-history theory. Quantifying the costs of reproduction in plants is challenging because reproductive and vegetative structures may draw on different pools of resources, and increased photosynthesis by vegetative structures changes the available resource pool (Reekie & Bazzaz 1987). Nonetheless, experiments demonstrate within-season trade-offs between growth and reproduction; for example, plants that delay reproduction allocate more resources to vegetative tissues (Delph & Meagher 1995, Rubin et al. 2019). Convincingly demonstrating across-season trade-offs between reproduction and growth in iteroparous perennials is particularly challenging because of methodological difficulties (Obeso 2002). To alleviate confounding factors like plant size, Horvitz & Schemske (1988) used a manipulative experiment to increase fruit yield in one year through pollen supplementation and found no detectable effect on survival or flowering in the subsequent year. An abundance of resources can limit the detection of costs; for example, in *Lychnis flos-cuculi*, investment in reproduction reduced subsequent fecundity in resource-poor sites only (Biere 1995). A multiyear field study on *Boechera stricta* revealed that fecundity selection and viability selection oppose each other in some environmental contexts (Wadgymar et al. 2017). Despite these challenges, an analysis of the literature by Obeso (2002) found mostly negative correlations between reproduction and one or more future life-history traits, providing support for the theoretically expected trade-offs.

Compromises among growth, maintenance, and reproduction mean that annuals should have greater reproductive effort than perennials, all else being equal. In comparisons of closely related annual and perennial species of *Plantago* (Primack 1979) and *Lupinus* (Pitelka 1977), annual taxa had higher reproductive effort than perennial taxa per vegetative unit. Across species, long-lived perennials have more variable fecundity than short-lived perennials (García et al. 2008). In a meta-analysis of 3,000 congeneric herbaceous annual/perennial species pairs, Vico et al. (2016) found that for both wild and domesticated pairs, plants with longer life spans preferentially allocated more resources to storage and belowground tissues that increase survival at the expense of seed mass. While ensuring adult survival negatively impacts fecundity in any given year, having more reproductive years typically leads to greater total fitness (Shefferson & Roach 2010).

The modular body plan of plants provides a mechanism for an architectural trade-off between life-history traits. Meristems may give rise to either vegetative or reproductive organs with considerable flexibility of form. Vegetative growth results in the proliferation of meristems, while sexual reproduction expends the meristem. Thus, the commitment of meristems to vegetative growth versus reproduction can generate negative correlations (Geber 1990), and the addition of vegetative structures early in development can influence survival and future reproduction (Kim & Donohue 2011). In *Mimulus guttatus*, differences in plant architecture between annuals and perennials may be due to differences in the fate of axillary meristems (Baker & Diggle 2011). Studies show that intraspecific differences between annual and perennial populations in this species are determined by pleiotropic and epistatic quantitative trait loci (QTLs) affecting both flowering time and vegetative growth (Friedman 2014, Friedman et al. 2015). In *Arabidopsis lyrata*, quantitative genetic analyses demonstrate that coordinated QTLs affecting early vegetative development have subsequent effects on reproduction (Remington et al. 2013). Thus, both morphological and quantitative genetic analyses suggest that developmental networks regulating meristem fate may be a proximate mechanism for trade-offs between vegetative and reproductive organs.

Quantitative trait locus (QTL): a region of the genome associated with phenotypic variation in a continuous trait

The classification of plants into discrete categories is somewhat arbitrary, and a number of species are facultatively annual or perennial, depending on the environment they experience. Individuals of the perennial herb *Arabis fecunda* can produce either a terminal inflorescence and then die or produce numerous inflorescences from axillary buds for many years. More individuals displayed a terminal strategy in stressful environments when the chance of survival and repeated reproduction declined, with evidence for both genetic and environmental components to the propensity for terminal flowering (Lesica & Young 2005). Water availability is often a key parameter for determining the likelihood of being annual versus perennial [e.g., *Streptanthus tortuosus* (Gremer et al. 2020), *Erysimum capitatum* (Kim & Donohue 2011)]. The degree of disturbance can also elicit facultative responses; for example, *Zostera marina* populations that are frequently disturbed have annual life histories (Reynolds et al. 2017). These examples suggest adaptive plasticity exists for life-history strategy where environmental stress causes individuals to trade off future fecundity for increased immediate reproductive effort. For plants to persist beyond annual strategies, they must maintain at least one vegetative meristem past the first growing season, potentially forfeiting some reproduction. However, it is not clear why some species are obligate annuals, when it would appear beneficial to keep growing when conditions are favorable. Whether there is a cost beyond the sacrifice of one meristem associated with being facultatively annual versus obligately annual is an open question.

3. CONTRASTING THE DEVELOPMENTAL GENETICS OF PHENOLOGY IN ANNUALS AND PERENNIALS

The frequent occurrence of evolutionary transitions among life histories in many lineages (see Section 4) suggests that the proximate molecular mechanisms responsible for key differences between annuals and perennials should be fairly easy to evolve. Therefore, identifying the individual genes and molecular pathways underlying flowering versus vegetative growth is an important component of understanding the evolution of plant life histories and can reveal potential evolutionary trajectories (Taylor et al. 2019). Here, I highlight how understanding the developmental and molecular mechanisms controlling key stages between vegetative and reproductive transitions can inform our understanding of evolutionary transitions between annual and perennial life forms and how this can be integrated with expectations from life-history theory.

3.1. Competence to Flower

Vernalization: the process by which flowering is promoted by prolonged exposure to the cold of a typical winter

After germination, a young vegetative plant is referred to as juvenile; this phase is characterized by specific leaf traits and an inability to transition to reproduction even if exposed to reproduction-promoting environmental cues (Hyun et al. 2017). The duration of the juvenile phase is typically very short in annuals, facilitating a rapid transition to flowering when exposed to appropriate environmental stimuli, such as photoperiod or vernalization. Perennials typically delay competence to flower from weeks to months, allowing plants to accumulate more biomass and more axillary meristems through branching prior to reproduction (Bergonzi & Albani 2011).

In both annual and perennial species, SQUAMOSA PROMOTER BINDING PROTEIN-LIKE (SPL) transcription factors and regulatory microRNAs (in particular, miR156) that control their expression play a central role in governing the juvenile-to-adult transition (Hyun et al. 2019). Levels of miR156 are high during early vegetative development in both the leaves and the shoot apical meristem and decrease with plant age, releasing the repression of SPL transcription factors (for reviews, see Bergonzi & Albani 2011, Hyun et al. 2017). The miR156/SPL system appears to be ancient and occurs in all angiosperms (Ortiz Morea et al. 2016). Therefore, a key difference between herbaceous annuals and perennials appears to be the evolution of genetic mechanisms in annuals to bypass the requirement for miR156/SPL to induce flowering so that they can rapidly acquire flowering competence (Hyun et al. 2019). In contrast, the gene *TERMINAL FLOWER 1* (*TFL1*) delays flowering and prolongs vegetative development (Albani & Coupland 2010) and therefore may be particularly important for perennials. Transgenic *Malus domestica* and *Populus trichocarpa* plants with reduced TFL1 function accelerated flowering by shortening the juvenile phase (Kotoda et al. 2006, Mohamed et al. 2010), and in perennial *Arabis alpina*, both *TFL1* and vernalization regulate flowering time (Wang et al. 2011).

Plant hormones, like gibberellic acid (GA), are an important component of regulating flowering; application of GA induces many plants to undergo stem elongation and flowering (Evans & Poethig 1995, Reekie 1997). However, a paradoxical observation is that GA has a positive effect on the switch to flowering in most species but a negative effect in some woody species (Boss & Thomas 2002). A mechanism was recently demonstrated in *A. thaliana*, where elevated GA promotes termination of the vegetative phase by increasing expression of transcription factors. These transcription factors then cause a reduction in GA that permits the accumulation of DELLA proteins to promote the expression of flowering genes (Yamaguchi et al. 2014). This dual role of GA may help explain why, in woody species, GA levels can be higher in juvenile shoot apices than in adult shoot apices (Hackett 1985) and why the application of exogenous GA can delay reproductive maturity (Lenahan et al. 2006). In grapevine (*Vitis vinifera*), a mutant cultivar that is insensitive to GA produces inflorescences along the length of the shoot where tendrils normally form, indicating that, in wild-type plants, GA inhibits flowering (Boss & Thomas 2002). GA is also implicated in regulating allocation to flowering versus branching and clonal growth, discussed in Section 3.3.

3.2. Flowering in Annuals and Perennials

Both annuals and perennials undergo a developmental switch from vegetative growth to flowering. In annuals, this transition occurs once and is followed by senescence and the death of the plant, while perennial plants cycle repeatedly, requiring reversion from reproductive to vegetative phases (**Figure 2**). Many plants show precisely controlled seasonal patterns in flowering, using environmental cues like changes in temperature and/or day length to generate a robust seasonal response (Andrés & Coupland 2012).

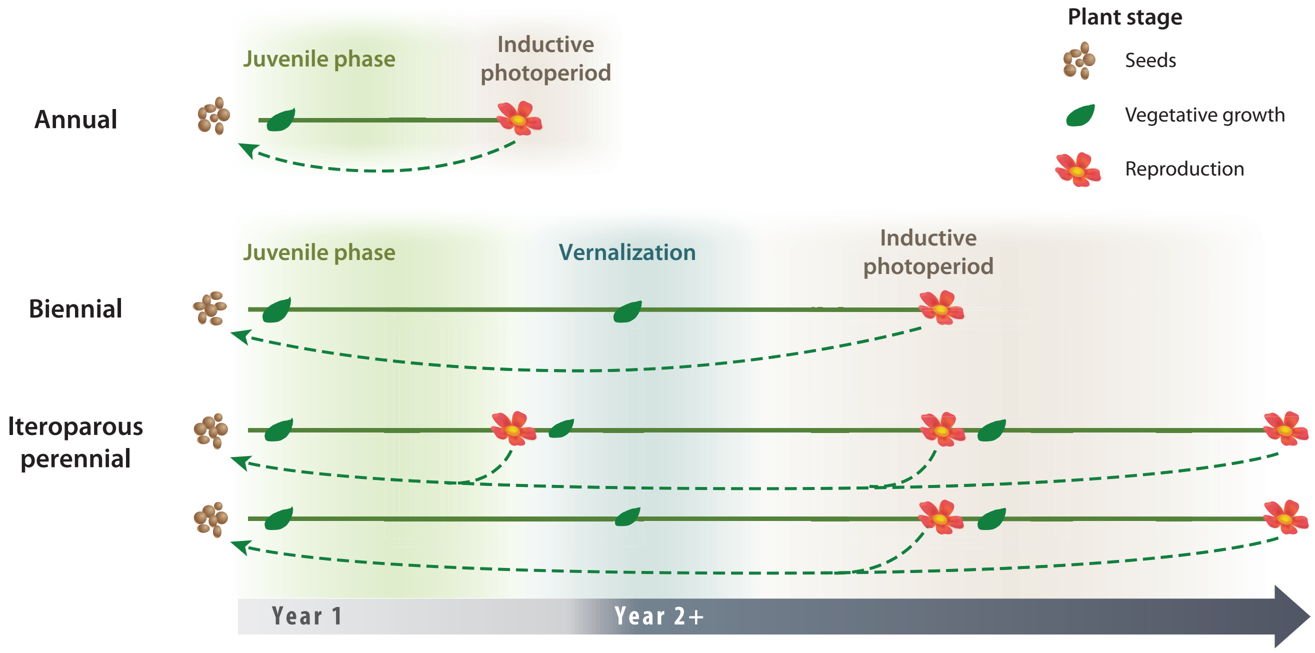

Figure 2

Conceptual diagram of the life cycle for annual, biennial, and iteroparous perennial plants. Plants in the vegetative stage are depicted with green lines, with a leaf indicating vegetative growth; flowering is depicted with orange flowers; and seeds are depicted with brown ovals. The dashed green lines represent the production of seeds that return to start the life cycle anew. The key seasonal components that have been studied from a developmental genetic perspective include the juvenile-to-adult transition (floral competency) and the photoperiod and vernalization pathways necessary for flowering. Iteroparous perennial plants must return to vegetative growth after flowering and require resetting of meristems or differential behavior of meristems on a single plant. Some iteroparous perennial species flower in their first year, while others have a longer juvenile phase or a requirement for vernalization prior to flowering.

3.2.1. Photoperiod. Predictable differences in day length are associated with the changing seasons, and many temperate plants use photoperiod as a cue for flowering phenology. The mechanisms of time measurement are best studied in *A. thaliana*, where photoperiod is measured in leaves by integrating information received from the circadian clock and light signaling such that CONSTANS (CO) activates *FLOWERING LOCUS T* (*FT*) under inductive long days (Suárez-López et al. 2001). Once induced, FT protein travels from the leaf via phloem to the shoot apical meristem, where it joins a protein complex that induces expression of meristem identity genes promoting flowering (Wigge et al. 2005). Research in *A. thaliana* has been complemented by studies in a variety of annual, perennial, and woody dicots and monocots (including barley, rice, ryegrass, poplar, morning glory, and tomato), where homologs of the *CO* and *FT* genes suggest that components of the photoperiod pathway are ancient and conserved (Andrés & Coupland 2012). Although annuals and perennials may use photoperiod cues in similar ways, their response depends on competence to flower being regulated by aging or exposure to cold.

3.2.2. Vernalization. Vernalization is the process by which extended exposure to cold renders a plant competent to flower, and it ensures that flowering occurs in the appropriate season. Unlike the photoperiod pathway, the vernalization pathway likely evolved multiple times as angiosperms diversified into temperate climates (Amasino 2010). Physiological studies of vernalization were first conducted in the biennial *Hyoscyamus niger*, where a requirement for prolonged cold exposure ensures plants flower only in their second year. Thus, vernalization provides a mechanism for controlling life history and ensuring adequate vegetative growth prior to flowering. For example, many wheat and barley species in Poaceae grow vegetatively for extended periods and will flower only after overwintering. The polycomb group protein VERNALIZATION2 (VRN2) blocks the long-day induction of *FT1* and prevents flowering prior to winter, and exposure to cold induces transcription of *VERNALIZATION1* (*VRN1*), which promotes inflorescence initiation (Fjellheim et al. 2014). Allelic variation in *VRN1* and *VRN2* has been linked to different vernalization requirements and life histories for wheat varieties that are adapted to particular environments (Eagles et al. 2009).

Similarly, allelic variation at key vernalization genes in *A. thaliana* causes populations to vary in their need for cold temperatures to regulate the flowering transition (Stinchcombe et al. 2004, Méndez-Vigo et al. 2011). In vernalization-sensitive *A. thaliana*, flowering is suppressed by FRIGIDA-mediated elevation of *FLOWERING LOCUS C* (*FLC*) expression (Amasino 2010). *FLC* is transcriptionally silenced by cold temperatures, allowing the shoot apical meristem to undergo the floral transition (Johanson et al. 2000). Relatively minor changes in gene regulation can underlie perennial cycling of the vegetative and flowering stages. In *A. alpina*, a perennial relative of *A. thaliana*, *PERPETUAL FLOWERING 1* (*PEP1*, an ortholog of *FLC*) is temporarily repressed by winter cold, but the chromatin modifications do not persist after vernalization (Wang et al. 2009). Thus, meristems that originate after cold exposure are inhibited from flowering, and repeated cycles of repression and activation of *PEP1* transcription facilitate seasonal flowering and limit the duration of the flowering period. Similar cycling expression patterns have been identified in other closely related perennial species, including *Arabidopsis halleri* (Aikawa et al. 2010), *Arabidopsis lyrata* (Kemi et al. 2013), and other species in the tribe Arabideae (Kiefer et al. 2017). Furthermore, Kiefer et al. (2017) compare sequence variation at *FLC* genes across annual and perennial Arabideae and suggest that perennials contain two types of *cis*-regulatory elements that repress or reactivate *FLC* orthologs after vernalization, with independent shifts to annuality evolving by deactivating a perennial element.

3.3. Achieving Cycles Between Vegetative Growth and Flowering in Perennials

Because perennial plants maintain vegetative growth after flowering, the perennial strategy requires differential behavior of meristems on a single plant such that some remain in the vegetative state, while others undergo the floral transition (Rohde & Bhalerao 2007, Albani & Coupland 2010). In perennials, existing meristems need to be reset to enable future flowering. A mechanism for this reset was demonstrated in *A. alpina*, where epigenetic modifications of *PEP1* do not persist after vernalization, in contrast to the annual *A. thaliana*, in which chromatin modifications on *FLC* are mitotically stable (Wang et al. 2009). In addition, plants develop a complex architecture where dormant buds are maintained and initiated during cold exposure to give rise to axillary branches (Lazaro et al. 2018, Vayssières et al. 2020). The capacity to reset meristems and maintain dormant buds may be a physiological limitation preventing obligate annuals from exhibiting facultative strategies.

The ability for perennial plants to cycle seasonally and commit only a subset of meristems to flowering may be due to genes with pleiotropic functions. For example, the gene *TFL1*, which plays a role in the duration of juvenility and inflorescence development, also determines whether axillary shoots commit to flowering or remain vegetative in perennials, as demonstrated in *Malus domestica*, *Populus trichocarpa*, *Fragaria vesca*, and *Lolium perenne* (Jensen et al. 2001, Kotoda et al. 2006, Mohamed et al. 2010, Tenreira et al. 2017). In poplar trees, the flowering-time genes *CO2* and *FT1* play additional roles in growth cessation and bud set with increased transcript abundance in response to short, cool days, and *Populus tremula* trees from different latitudes in Europe varied in the day length necessary to induce transcript accumulation that leads to growth cessation

(Böhlenius et al. 2006). In *Populus deltoides*, the gene *FT2* is involved in the first initiation of flowering and also in the seasonality of vegetative growth and flowering (Hsu et al. 2006), facilitating the sequential phase change between vegetative and floral buds. These examples provide potential mechanisms for iteroparity in perennials.

Many perennials establish secondary rounds of vegetative growth from meristems on stolons or rhizomes, and there may be a direct trade-off between vegetative growth versus flowering. For example, in strawberry (*Fragaria* spp.) grown under long days, vegetative reproduction can occur at the expense of fruit yield, and the gibberellin hormones can alter this balance. A mutation in woodland *Fragaria vesca* revealed that a trade-off between the fate of axillary meristems between flowering and runner production is due to a deletion in the gibberellin 20-oxidase (*GA20ox*) gene (Tenreira et al. 2017). A recent genomic analysis comparing annual and perennial *M. guttatus* discovered *GA20ox2* as a major allele frequency outlier between the ecotypes (Gould et al. 2017). Application of synthetic GA caused perennial plants to assume an annual-like morphology (Lowry et al. 2019). Thus, the shift in allocation between growth and reproduction may be due to pleiotropic genes regulating hormone production.

Understanding the developmental genetic mechanisms regulating key differences between annuals and perennials could help predict the evolution of different strategies in response to environmental conditions and help explain why transitions occur more frequently in some lineages than others. Nonetheless, the research connecting these fields is currently restricted to a few well-studied groups, and for most of the angiosperms, we have little understanding of the physiological mechanisms underlying evolutionary transitions between annual and perennial strategies.

4. MACROEVOLUTIONARY PATTERNS OF TRANSITIONS BETWEEN ANNUALITY AND PERENNIALITY

The extent of variation in life history and the relative ease of evolving regulatory networks that alter patterns of flowering and growth suggest that evolutionary flexibility and transitions between different strategies are common. Annuals make up approximately 10% of angiosperms, and although not evenly distributed across families, they have evolved numerous times from perennial ancestors (Angiosperm Phylogeny Group 2016). Annuality is a derived condition in more than 100 plant families from more than 30 orders of angiosperms (Angiosperm Phylogeny Group 2016), and it is conceivable that annuality has evolved thousands of times, making it one of the most important reproductive transitions. The longstanding view is that the woody habit and accompanying perennial life history strategy are the ancestral condition in angiosperms, followed by evolution of herbaceousness and then annuality (Stebbins 1950, Soltis et al. 2013) (**Figure 1**). However, recent findings (discussed in Section 4.1) suggest than transitions from annual to perennial strategies may also occur in herbaceous lineages.

4.1. Phylogenetic Comparative Approaches

Within specific taxa, ancestral-state reconstructions using phylogenetic approaches have generally found that annuals are derived from perennial ancestors, and in many cases, multiple origins of annual species are reported within a genus. For example, *Nemesia* (Scrophulariaceae), which comprises approximately 65 species of annual and perennial herbs and shrubs native to southern and tropical Africa, is approximately 75% annual with at least four independent transitions to annuality (Datson et al. 2008). Similarly, in *Veronica* (Plantaginaceae), approximately 10% of the 450 species are annuals, representing at least six independent origins (Wang et al. 2016). Other examples where annuality has evolved repeatedly from perenniality within a single genus include

Sidalcea [Malvaceae (Andreasen & Baldwin 2001)], *Houstonia* [Rubiaceae (Church 2003)], and *Bellis* [Asteraceae (Fiz et al. 2002)].

Contrary to classical interpretations of life history evolution in plants, in some genera, pereniality has evolved from annual ancestors. This is especially common on oceanic islands (Carlquist 1974), most famously in the silversword/tarweed group (Baldwin 2007), in which island endemic clades have repeatedly evolved perennial life forms (Nürk et al. 2019). Other examples of derived perenniality include clades that tend to show considerable lability with transitions in both directions; for example, in Saxifragales there are shifts from woody perennials to herbaceous perennials followed by transitions in both directions between herbaceous annuals and perennials (Soltis et al. 2013). Similarly, in the perennial *Castilleja* clade, phylogenetic reconstruction suggests that perenniality evolved a single time from an annual ancestral lineage and that there have been some reversions to annuality within the perennial clade (Tank & Olmstead 2008). The herbaceous Montiaceae group also shows considerable flexibility of life history that is strongly associated with temperature-niche evolution (Ogburn & Edwards 2015). In the next section, I discuss how evolutionary transitions in life history are driven by ecological conditions.

4.2. Environmental and Biogeographic Associations

The early diverging angiosperms were woody perennials confined to tropical and subtropical regions, with herbaceous plants gaining prominence at the start of the Tertiary period and spreading into temperate zones (Ricklefs & Renner 1994). Annuals are most highly represented in temperate regions; however, at the highest latitudes and under alpine conditions, long-lived perennials tend to dominate, and annuality is rare. Thus, there exists a nonlinear pattern in the representation of annual versus perennial plants at different latitudes and elevations, with annual plants being underrepresented in the tropics (particularly the aseasonal tropics) and alpine and arctic ecosystems (Ricklefs & Renner 1994). The tropics and many oceanic islands experience climatic moderation that creates year-round growing seasons that favor perenniality and longer plant life cycles (Nürk et al. 2019), while alpine and arctic ecosystems have very short growing seasons that favor perennials with dormant underground plant structures that can rapidly capitalize on brief growing seasons (Billings & Mooney 1968).

Theoretical models predict that annuality evolves as an adaptive response to unpredictable environments, including frequently disturbed habitats, high temperatures, and seasonal droughts (Stearns 1992). Empirical data supports this idea, with a shift to annual life histories often occurring in hot and dry conditions that would adversely affect adult perennial plants. For example, Evans et al. (2005) used phylogenetically independent contrasts to demonstrate that in a clade of evening primroses (*Oenothera*), transitions to the annual habit were associated with high summer temperatures and increased winter aridity. Similarly, three independent origins of annuality evolved in *Bellis* in the Mediterranean basin in areas of summer drought (Fiz et al. 2002), and perenniality and annuality have repeatedly evolved in *Heliophila*, with annuals occurring in environments with more frequent drought (Monroe et al. 2019). In *Nemesia*, at least four independent shifts from perennial to annual life history were all associated with a shift in climate from summer rainfall to summer drought and winter rainfall (Datson et al. 2008). A high relative growth rate usually accompanies the evolution of an annual life history, facilitating survival in shorter growing seasons (Verboom et al. 2004).

Annuals are especially common in desert and Mediterranean-climate regions (e.g., the southwestern USA, the Middle East, Chile) in environments that experience severe or prolonged drought. Here, the annual habit serves as a drought-evasion mechanism, ensuring that plants complete their life cycle within a limited time, usually corresponding to a brief rainy season that stimulates germination. Thus, they tend not to be drought tolerant in their vegetative state, but their seeds remain viable during prolonged conditions of aridity. A key characteristic of desert annuals is their prolonged seed dormancy and potential for variable germination strategies (diversified bet hedging) to reduce variance in fitness because of unpredictable environments (Venable 2007). Bet hedging can also be an important feature of iteroparous perennials; prolonged dormancy belowground may benefit survival by allowing plants to avoid aboveground stress (Gremer et al. 2012). In general, unfavorable growing conditions for part of the year do not preclude perennials but favor selection of seasonally dormant structures, such as protected buds, belowground storage, or endodormancy.

Bet hedging: an evolutionary strategy to optimize fitness in variable environments by reducing variance in fitness between years

Endodormancy: a physiological state characterized by growth inhibition that occurs in response to cold temperatures in woody species

Reproductive assurance: increase in seed set caused by self-fertilization when pollinators and/or potential mates are scarce

Pollen limitation: reduced reproductive success caused by an inadequate quantity or quality of pollen such that some ovules remain unfertilized and developing embryos do not compete for resources

5. EVOLUTIONARY CONSEQUENCES OF LIFE HISTORY FOR REPRODUCTIVE SYSTEMS AND GENOME EVOLUTION

The differences in life span and investment in reproduction and growth between annuals and perennials generate myriad consequences for the evolution of mating systems, sexual systems, and genomes. Because annual plants must set seed in the year they germinate, their fitness is entirely dependent on the success of those progeny. In contrast, fitness in iteroparous perennials is a function of both seed set (and progeny success) and parental survival. This key difference in life span and routes to fitness generates a variety of consequences for floral display, mating patterns, and genome evolution.

5.1. Self-Fertilization

One of the most widely recognized trait associations is between annuality and self-fertilization (Stebbins 1950, Barrett & Harder 2017), and this association is supported by phylogenetic analyses. A recent analysis of outcrossing rates for taxa in diverse biogeographic regions reported that variation in life form was largely responsible for latitudinal patterns in mating system (Moeller et al. 2017). Using the data provided in this paper, I show the markedly different distribution of outcrossing rates in annual and perennial taxa ($F_{1,153} = 25.33$, $P < 0.001$) (**Figure 3*a***; see figure caption for statistical details). While these large-scale patterns are well established, they are confounded by other aspects of species differences, and ideally, a comparison of outcrossing rates among intraspecific annual and perennial populations would be most informative. A recent study of *Incarvillea sinensis* found that outcrossing rates (t_m) were significantly higher in perennial (mean $t_m = 0.76$, $n = 8$) than annual (mean $t_m = 0.09$, $n = 8$) allopatric populations, and these differences were maintained in five sympatric populations where annual and perennial plants coexisted (Y. Ma, S.C.H. Barrett, F.-Y. Wang, J.-C. Deng & W.-N. Bai, manuscript in review). Such studies can help to clarify the ecological mechanisms responsible for the common associations between annuality and self-fertilization.

One explanation for the association between annuality and selfing was first proposed by Stebbins (1950) and Baker (1955) who contended that annual plants are more often colonizers of open and disturbed habitats and are more likely to succeed if they are selfing. Because the lifetime fitness of annuals is more vulnerable to poor environmental conditions during the reproductive season, self-fertilization may be favored through reproductive assurance (Eckert et al. 2006). This contrasts with iteroparous perennials, where yearly fluctuations in seed set reduce lifetime fitness less than for annuals (Lloyd 1980). Moreover, the unpredictable and seasonally dry conditions in which annuals commonly occur are often associated with low population density and/or unreliable pollinator service, which would similarly select for selfing to alleviate pollen limitation and reproductive failure (Munoz et al. 2016). Thus, correlations between habitat characteristics and plant

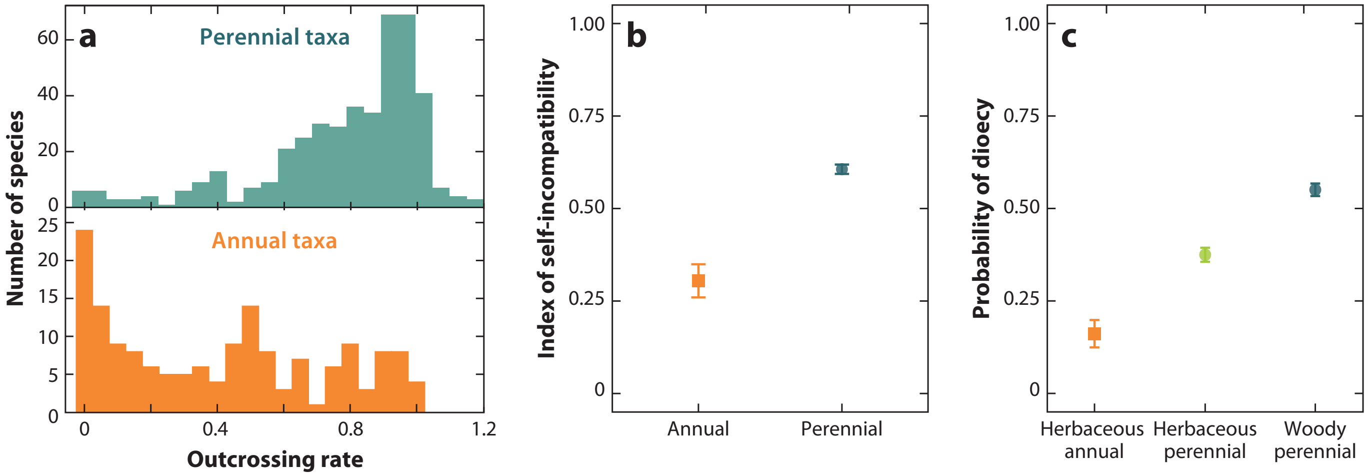

Figure 3

Mating and sexual system correlates with plant life history. (*a*) Distribution of outcrossing rates (t_m) for annual ($n = 160$) and perennial ($n = 438$) taxa. Data from Moeller et al. (2017). (*b*) Index of self-incompatibility for annual ($n = 76$) and perennial ($n = 945$) species. Means and standard errors are estimated from a regression model. Data from Raduski et al. (2012). (*c*) Probability of dioecy in annual herbaceous species ($n = 99$), perennial herbaceous species ($n = 648$), and perennial woody species ($n = 859$). Means and standard errors are estimated from a logistic regression model. Data from the Tree of Sex Consort. (2014). This last data set heavily overrepresents the occurrence of plants with unisexual flowers, as it was compiled to focus on taxonomic groups exhibiting variation. Thus, it should not be interpreted as representative of the overall frequency of dioecy in angiosperms but only as a description of the relative frequencies in plants with different life forms. For each data set, I constructed a pruned phylogeny for the taxa using Phylomatic, version 3, and the phylogeny of Zanne et al. (2014), including branch lengths. I then used the R packages caper (Orme et al. 2018) (panels *a* and *b*) and phylolm (Ho & Ane 2014) (panel *c*) to conduct phylogenetic generalized least squares analyses to assess statistical significance.

life histories seem likely to be the major cause of the associations with mating systems (Barrett & Harder 2017).

Despite a longstanding recognition of the general association between annuality and self-fertilization, the evidence for the order of these transitions is sparse. The ecological associations described above suggest that the evolution of selfing occurs in annuals. Indeed, Barrett et al. (1996) demonstrated that autogamy evolved repeatedly within annual lineages of *Gilia* species. Similarly, in *Amsinckia*, *Camissonia*, *Clarkia*, *Gayophytum*, *Limnanthes*, and *Lolium*, both outcrossing and selfing annual species occur, with the shift to selfing likely to be a derived condition; however, explicit phylogenetic approaches have been applied only to some of these examples. The need for phylogenetic analysis is demonstrated by Bena et al. (1998), who found that the order and direction of transitions are sensitive to the weighting applied to different transitions. Contrary to the examples above, annuality evolved only in selfing lineages in *Medicago* (Bena et al. 1998). This order of events is supported by theory showing that selfing increases female fitness gain, which selects for both higher female allocation and greater total reproductive effort (Zhang 2000). This, in turn, increases the optimal allocation to reproduction at the expense of survival, provided inbreeding depression is less than one-half. Similarly, Lesaffre & Billiard (2020) show in a theoretical model that self-fertilization can facilitate the evolution toward shorter life spans when inbreeding depression affects adult survival. Thus, selfing can, in principle, drive the evolution of an annual life history, although this mechanism has yet to be demonstrated empirically.

Inbreeding depression: reduction in viability and fertility of offspring from self-fertilization or other forms of inbreeding compared with cross-fertilized offspring

In contrast to focusing on the benefit of selfing in annuals, Lloyd (1992) emphasized the costs of selfing in perennials. Perennials pay a cost when selfing increases seed set in one year at the expense of future survivorship and outcrossing in subsequent years (Morgan et al. 1997). Demonstrating that seed set in one year induces between-season costs is challenging due to the complex trade-offs. Nonetheless, between-year seed discounting in perennials and the costs of adult inbreeding depression (see Section 5.2) can theoretically cause an association between perenniality and outcrossing without the need for reproductive assurance (Morgan et al. 1997). Outcrossing might also be particularly advantageous for perennial species that occupy competitive and heterogeneous environments in which offspring quality is important and, indeed, a survey of ∼2,000 species reported that more competitive species were more likely to outcross and be perennial (Munoz et al. 2016).

Self-incompatibility (SI): a physiological mechanism that prevents fertile hermaphrodite plants from setting abundant seed following self-pollination

5.2. Mutational Load and Inbreeding Depression

Several features of perennial life histories may influence inbreeding depression. In all plants, mutations occurring in somatic tissues may be passed on to offspring due to the absence of a segregated germline. Because the per-generation mutation rate is a function of the number of mitotic divisions between zygote formation and gamete production (Scofield & Schultz 2006), older organisms should accumulate more mutations. Long-lived perennials undergo more cell divisions and should therefore accumulate a greater number of somatic mutations per generation compared to short-lived and small-statured annuals (Scofield & Schultz 2006). A consequence of this difference in mutation rate is that perennials may experience greater mutational load and exhibit higher levels of inbreeding depression than annuals.

In addition to the difference in per-generation mutation rate, perennials may suffer more inbreeding depression due to their increased life span. Empirical surveys demonstrate that inbreeding depression is compounded over life-cycle stages (Husband & Schemske 1996), and meta-analyses suggest that perennials and long-lived woody species experience higher inbreeding depression than annuals (Angeloni et al. 2011). Theoretical analyses corroborate the hypothesis that longevity amplifies the effects of inbreeding depression on survival (Morgan et al. 1997, Lesaffre & Billiard 2020). With longer generations, mutational load is increasingly determined by recessive, rather than partially dominant, mutations through a selective sieve process where more recessive mutations are less effectively removed (Morgan 2001). Higher mutational load also means that when selfing does occur, severe inbreeding depression leads to the failure of selfed offspring, which prevents deleterious recessive mutations from being purged as a result of selective interference (Lande et al. 1994). Evidence for these consequences of increased life span comes from studies showing that, even among perennials, self-incompatible species generally live longer than species that have the capacity to self-fertilize (Ehrlén & Lehtila 2002) and that woody species generally have higher outcrossing rates than herbaceous perennial species (Barrett et al. 1996, Duminil et al. 2009, Moeller et al. 2017). The inbreeding coefficients of long-lived perennials are lower than expected from their selfing rates, suggesting strong selection against inbred individuals (Scofield & Schultz 2006, Duminil et al. 2009).

5.3. Self-Incompatibility and Pollen Limitation

The most common and phylogenetically widespread mechanism for the prevention of self-fertilization is self-incompatibility (SI). Raduski et al. (2012) reported a bimodal distribution for the index of self-incompatibility in 1,238 angiosperm taxa and a significant difference between the distributions of annual and perennial species. I use their data here to show that perennials have more species with greater SI than annuals ($F_{1,592} = 10.58$, $P < 0.01$) (**Figure 3*b***; see figure caption for statistical details). While the breakdown of SI associated with annual lineages (Raduski et al. 2012) likely contributes to higher selfing in annuals (**Figure 3*a***), other differences including reduced herkogamy and dichogamy also contribute to a greater facility for autonomous self-pollination in annuals compared to closely related perennials (Vos et al. 1994; Y. Ma, S.C.H. Barrett, F.-Y. Wang, J.-C. Deng & W.-N. Bai, manuscript in review).

Dioecy: a sexual polymorphism in which populations are composed of female and male individuals

Geitonogamy: self-pollination resulting from pollen transfer between flowers on the same individual

Self-incompatible hermaphroditic plants incur substantial fitness costs to male function due to pollen discounting, since pollen transferred between flowers on the same individual represents a lost outcross mating opportunity. The female costs of SI depend on the degree of pollen limitation and whether seed set is limited by the receipt of compatible pollen. What is the evidence for pollen limitation in perennial plants? Knight et al. (2005) demonstrate a trend for greater pollen limitation among iteroparous than semelparous plants (although this was not significant after controlling for phylogenetic relationships), and significantly more pollen limitation for woody species than herbs. The overall pattern of both higher SI and greater pollen limitation in long-lived perennials suggests that the fitness costs of selfing are substantial and that long-lived species are better able to endure fluctuations in pollen receipt (Knight et al. 2005). Iteroparous perennials may also buffer against stochasticity in reproductive success by being able to store resources for the future in poor pollination years or draw on past savings in years with good mating success (Ida et al. 2015).

5.4. Dioecy

A well-established association occurs between dioecy and perenniality, particularly in woody perennials (Ricklefs & Renner 1994, Vamosi et al. 2003). However, even within herbaceous groups, dioecy appears to be more common in perennials than in annuals. To quantify these associations, I used the Tree of Sex Consort. (2014) data set to examine the frequency of hermaphroditism (excluding monoecy) versus dioecy in annuals, herbaceous perennials, and woody perennials (excluding shrubs). I included a subset of the data ($n = 1{,}606$) with complete information for these categories. My results corroborated the high incidence of dioecy in woody taxa but also indicated that herbaceous perennials exhibit significantly more dioecy than annuals ($F_{2,856} = 4.20$, $P < 0.05$) (**Figure 3*c***; see figure caption for statistical details). The most common proposed mechanism for the association between dioecy and perenniality is the increased opportunity for geitonogamy by larger plants with more simultaneously open flowers. Thus, dioecy may evolve to avoid inbreeding. However, this pattern could also arise due to differential extinction, as perennial dioecious lineages have a lower extinction risk than annual dioecious lineages because of their ability to persist through years of poor pollinator service (Vamosi & Otto 2002, Wilson & Harder 2003). A recent study by Dorken & Van Drunen (2018) proposes that negative correlations between sexual reproduction and both vegetative growth and survival in perennials can promote the evolution of dioecy even when trade-offs between male and female sex function are indirect (e.g., they draw on different resource pools), suggesting that a perennial strategy may expand the circumstances under which theory predicts the stable evolution of unisexuality.

5.5. Genome Size and Polyploidy

Genome sizes vary greatly in plants, primarily due to the presence of different amounts of noncoding, repetitive DNA, including transposable elements. In general, genome size is correlated positively with cell size and negatively with cell division rate; therefore, an association may exist between generation time and genome size (Bennett & Leitch 2005). The amount of DNA content may place a lower limit on the minimum generation time. Indeed, taxa with very large genomes all have long generation times and are perennial, never annual (Bennett & Leitch 2005). Increases in genome size could result in perenniality if slower cell division means that the life cycle cannot be completed within a single season (Müntzing 1936), although clear empirical evidence of this causal association has yet to be demonstrated.

Polyploidy is disproportionately common among perennials, particularly herbaceous perennials (Gustafsson 1948, Stebbins 1950), and analyses using phylogenetic comparative methods support this association (Van Drunen & Husband 2019). Mechanisms underlying the association are unclear. One scenario suggests that the ability to reproduce iteroparously predisposes species to polyploid establishment because they have more time to find compatible mating partners and more easily overcome minority cytotype exclusion that occurs when they first arise (Husband 2000). Alternatively, the origin of perenniality could be a direct consequence of a whole-genome duplication event, for example, due to increased cell size, lower cell division rate, and slower growth rate (Müntzing 1936), or a result of changes in gene expression of key regulatory genes that alter plant architecture or flowering (Osborn et al. 2003). Overall, different mechanisms appear to have been important in particular clades, and finding general trends may remain elusive (Van Drunen & Husband 2019). A recent biogeographic study of polyploidy finds that polyploid frequency increases with distance from the equator in a pattern that mirrors the distribution of mating systems (Moeller et al. 2017); this association is largely mediated by variation in the distribution of herbaceous perennials versus annuals (Rice et al. 2019).

Polyploidy: the condition of possessing more than two complete sets of chromosomes

5.6. Speciation and Evolutionary Rates

Rates of speciation vary extensively among angiosperms, with long-lived perennial herbs and woody species experiencing slower speciation rates (Smith & Donoghue 2008). This difference in speciation may be due to the increased generation time of long-lived perennials. In perennials, speciation more often occurs via the isolation of large allopatric populations that slowly develop isolating mechanisms, facilitating hybridization following secondary contact (Whittemore & Schaal 1991). In contrast, the shorter generation time of annuals increases the potential for genetic recombination, and chromosomal rearrangements are much more common in annual species than perennial species (Archibald et al. 2005). Accordingly, annuals exhibit higher speciation rates and more frequently develop postzygotic reproductive isolation than perennials. On the other hand, Soltis et al. (2013) found that the greater net diversification of annuals in Saxifragales is driven by significantly lower extinction in annual versus perennial lineages. Although the mechanism for lower extinction rates in annuals is unclear, they propose that seed dormancy in annuals might decrease extinction risk (Soltis et al. 2013).

Comparisons of molecular evolutionary rates among plant lineages generally find that annual plants show elevated rates of molecular evolution compared with perennials, but the causes behind these patterns remain unclear. For example, Bousquet et al. (1992) found no significant differences between woody and herbaceous perennials in their rate of synonymous and nonsynonymous substitutions of *rbcL* gene sequences. They therefore rejected generation time as a putative cause and proposed that larger effective population sizes in perennials contribute to their slower rates of evolution. However, Smith & Donoghue (2008) used phylogenies of five angiosperm clades to demonstrate that rates of molecular evolution are consistently lower in trees and shrubs, compared with related herbaceous species, invoking generation time as the primary mechanism. In a comparison of annual and perennial *Sidalcea* (Malvaceae) species, both generation time and differences in populations sizes can explain evolutionary rate differences (Andreasen & Baldwin 2001). Part of the reason why generation time may be insufficient as a predictor of rate variation could be the uncertainty and imprecision in measuring this life history trait.

6. CONCLUSIONS AND FUTURE DIRECTIONS

The evolutionary transition between a perennial and annual life history is exceptionally common among angiosperms. Ancestral state reconstructions using phylogenetic approaches have generally found that annuals are derived from perennial ancestors; however, the evolution of perenniality has also been demonstrated. Empirical data supports the theory that the evolution of annual life histories is associated with arid, disturbed, or unpredictable environments in which adult survival is low or variable. Empirical evidence supports the theoretical expectation for trade-offs between reproduction and growth/survival, and the modular body plan of plants provides a proximate phenotypic mechanism for this trade-off. Nonetheless, resource availability can mask these trade-offs and it is not clear why more annuals do not perennate under favorable conditions. Future research could use common garden studies of annuals and perennials with environmental manipulation to investigate the plasticity of life histories and the potential costs associated with facultative strategies.

The fundamental difference in the number of reproductive episodes and mortality in annuals and perennials results in an association between life history and reproductive systems: Perennials have higher outcrossing rates and greater frequency of SI, dioecy, and polyploidy. In addition, perennials tend to experience stronger inbreeding depression and slower evolutionary rates. Despite these well-recognized patterns, we do not fully understand the reasons for these associations nor their evolutionary history. Future work should use comparative methods to investigate associations between sexual systems (e.g., SI or dioecy) and life history to determine patterns of correlated evolution and the sequence of the origination of traits within lineages. Experiments are necessary to understand the selective mechanisms underlying these patterns. Experimental approaches could demonstrate whether selection for selfing increases female allocation at the expense of survival, leading to annuality, or identify the extent to which differences between annuals and perennials in resource allocation trade-offs between growth and reproduction affect sex allocation trade-offs between female and male function. Experiments with neo-polyploids could be used to investigate the causes and consequences of genome doubling on perenniality. Experimental manipulations provide a comprehensive means to ravel the mechanisms underlying common trait associations and examine their fitness consequences.

Understanding the molecular mechanisms of flowering and the seasonal cycling of reproduction and growth provides insight into the roles of pleiotropy and epistasis in regulating life-stage switches and the developmental physiology underlying evolutionary trade-offs. Incorporating molecular genetic studies in diverse taxa will help to identify the proximate genetic mechanisms of transitions between annual and perennial forms, including demonstrating whether similar genes are the targets of selection in diverse lineages. I encourage researchers to connect the genetic mechanisms underlying growth and reproduction (for example, pleiotropy) with theoretical predictions (e.g., trade-offs) to understand life-history evolution. A perspective that integrates genetic mechanisms can help guide research on why transitions occur more frequently in some lineages than others, how complex traits evolve in different ecological conditions, and how evolution acts on naturally segregating variation to produce annual versus perennial life histories.

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