

We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

4,800

Open access books available

122,000

International authors and editors

135M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities



WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com



Roles of the Environment in Plant Life-History Trade-offs

Yang Liu, Jeffrey L. Walck and Yousry A. El-Kassaby

Additional information is available at the end of the chapter

<http://dx.doi.org/10.5772/intechopen.70312>

Abstract

Variation in plant life-history and functional traits at between- and within-species levels has key ecological consequences, in which environmental settings impose strong selective pressures and play a vital role throughout life cycles. Our general notion for plant life-history strategies may be that, relative to tall, long-lived plants, short-lived species have features of small stature, small-seededness, rapid growth, and low seedling survival (*k*- versus *r*-selection). Rate of evolution may be an important agent of selection and annuals evolve more rapidly than perennial congeners. These empirical observations prompt a suite of enticing questions, such as how do life-history traits interplay with functional trait at late stages of regeneration? what are the primary trade-offs in a cohort of key life-history traits that may have undergone stabilizing selection? and how do environmental filters differently affect adaptive trait variation in annuals and perennials? In this chapter, we intend to address aforementioned questions via assembling our updated knowledge with emphasis on seed mass and temporal and spatial dimensions of seed dispersal. Through such synthesis, we wish to raise awareness about life-history trade-offs and provide a holistic understanding of the extent to which climate change is likely to impact plant adaptation and eco-evolutionary trajectories of life-history phenotypes.

Keywords: plant life histories, life-history trade-offs, seed mass, seed number, seed dormancy, seed dispersal syndrome, seed emergence, seed persistence, soil seed bank, life-cycle transitions, climate change

1. Introduction

Life-history traits, known as fitness components due to their predictable monotonic relationship with fitness, are related to the timing and success of development, reproduction, and

senescence throughout the life cycle [1]. The environment has appreciable influences on plant life histories and in the life cycle, the timing of life-history traits (e.g., flowering, seed set, seed mass, seed number, seed dormancy intensity [i.e., delayed onset of germination], seed emergence, etc.) are covaried and thus probably coevolved. Examples for the interplay between the environment and life-history traits at ecological and/or evolutionary levels are instantiated as follows.

- At a global scale, seed dormancy tends to decrease and seed size to increase toward the equator [2–4].
- Life cycles with early flowering, small seeds, deep dormancy, and slow germination are associated with habitats exposed to high temperature, low rainfall, and high radiation [5]. (Note: warming selects for higher optimal photosynthetic temperatures.)
- Lower temperatures with as little as 1°C differences ($T_{\text{critical}} = 15^{\circ}\text{C}$) to the maternal plant in *Arabidopsis*, on the contrary, tend to enhance final seed dormancy levels [6–9].
- Under natural conditions, a given plant may produce seeds with different levels of dormancy in association with a particular temperature it has experienced during seed development [10].
- Variations in seed dormancy and mass often have a concomitant effect (reviewed by [4]) and are correlated in a negative manner [5, 11–15].
- Species showing very fast germination behavior have (very) small seeds and little or no endosperm, and there is a clear relationship between the phenomenon of very fast germination and high stress habitats (e.g., arid, saline, or in active floodplains), where seeds can rapidly exploit temporarily favorable conditions for germination [16].
- There is a positive correlation of relative embryo length with germination speed and negative correlations with the amount of habitat shade, longevity and precipitation [note that small embryo sizes are typical of primitive taxa] [17].
- Climate change is accelerating plant developmental transitions in temperate environments and advanced flower timing increases dormancy intensities [5, 8, 18].
- Early germination increases seed fecundity due to prolonged vegetative growth and nutrient accumulation but may also bring about high seedling mortality [5].
- There is a strong relatedness between seed mass and the depth of burial from which seedlings emerge [19, 20] and germination of large seeds is strongly facilitated by temperature fluctuations, ensuring germination after deep burial or in litter layers [21–23].
- There exists a negative correlation between seed dormancy and longevity [24] with small seeds persisting longer in soil seed banks than large seeds [25].
- There are strong correlations between seed mass and dispersal syndromes and their correlations hinge on dispersal vectors [26, 27].

Some life-history traits may have reciprocal effects with functional traits at late life stages of regeneration. Environmental challenges, mostly to the maternal plant, influence the resources

Trait one	Trait two	Correlation	References	Notes
Seed dormancy	Seed mass	-	[5, 11–15]	(1)
Seed dormancy	Seed persistence	No?	[143]	(2)
Seed dormancy	Seedling survival	-	[5, 14]	
Seed dormancy	Seed longevity	-	[24]	(3)
Seed mass	Time to seedling emergence given favorable germination conditions	+	[144]	
Seed mass	Seedling growth rate	-	[145–147]	
Seed mass	Maternal plant size	Neutral or +	[28, 148, 149]	(4)
Seed mass	Seed number per lifetime	No	[150]	
Seed mass	Seedling survival	No or weak +	[122, 123]	
Plant size	Time to reproductive maturity	+	[150]	

Notes: (1) In general, species that produce light seeds are more likely to possess some type of seed dormancy [69, 142]. Other correlations were also documented and these inconsistencies may be explained by an incomplete consideration of other covarying factors (e.g., dispersal, fire, and predation) [13] or by phylogenetic constraints [151]. Variation in seed size and dormancy often results from a seed position effect within an inflorescence and within a dispersal unit [35, 50] and this also contributes to uncertainties of their associations. At molecular levels, the parent-of-origin effects on seed traits (e.g., dormancy and size), which are regulated by chromatin remodeling, have been documented for crossing between plants in different ploidy and mutants defective at reproduction [152].

(2) Such correlation remains in the question, as the cited study did not measure whether “the degree of dormancy” was related to persistence. Contrasted with seed release at maturity, canopy seed storage (i.e., serotiny) is reviewed in [153] and we do not extensively discuss canopy-stored seed banks in this chapter. Global warming is expected to reduce seedling emergence for some species [154, 155]. Moreover, the evolution of seed dormancy is favored by high seed persistence in the soil seed bank to alleviate the cost of delayed germination [156]. Both Cohen and Ellner’s models suggested that an increase in seed survivorship selects for a low seed germination [88–90]. Soil temperature is the dominant environmental factor controlling the depth of seed dormancy during cycling in imbibed seeds [157]. Climate change engenders long-term exposure to high soil temperatures, which may reduce seed survival, thus selecting for decreased levels of seed dormancy [158]. Taken together, climate change may increase seed numbers in the life cycle and decrease dormancy levels due to increased seed mortality.

(3) Dormancy cycling coupled to seed longevity represents a bet-hedging strategy through persistence in the soil seed bank [159, 160]. As a consequence, seed persistence may be not simply associated with either seed dormancy or longevity.

(4) The mother plant has a significant influence over seed traits and instances have been documented for more than 10 decades. Factors such as age of the mother plant, position of the seed in the fruit, inflorescence, or canopy can affect seed properties, often accompanied by a dimorphism either of the seeds themselves or the fruits in which they arise [161].

Table 1. A summary of correlations of adaptive traits.

that are packaged into seeds (seed size) and may be critical for germination and initial seedling growth. For instance, small-seeded species have small plant size (e.g., a positive correlation between seed mass and plant height [28]). Larger plant size, in turn, has higher annual photosynthetic incomes, giving the plant more energy to allocate to seed yield (increased number, heavier mass, or a trade-off between the two in life cycles). Rather, there are studies reporting that seed mass, nature plant height, and leaf mass per unit area have little intercorrelations [29] and that seed dormancy strategy is largely independent of vegetative functional traits and range characteristics [30]. Those inconsistent reports supply us with clues to studying the interaction between adaptive traits in a broader scope (e.g., controlling for phylogeny, more species from different taxa, and/or more traits at different stages of life cycles).

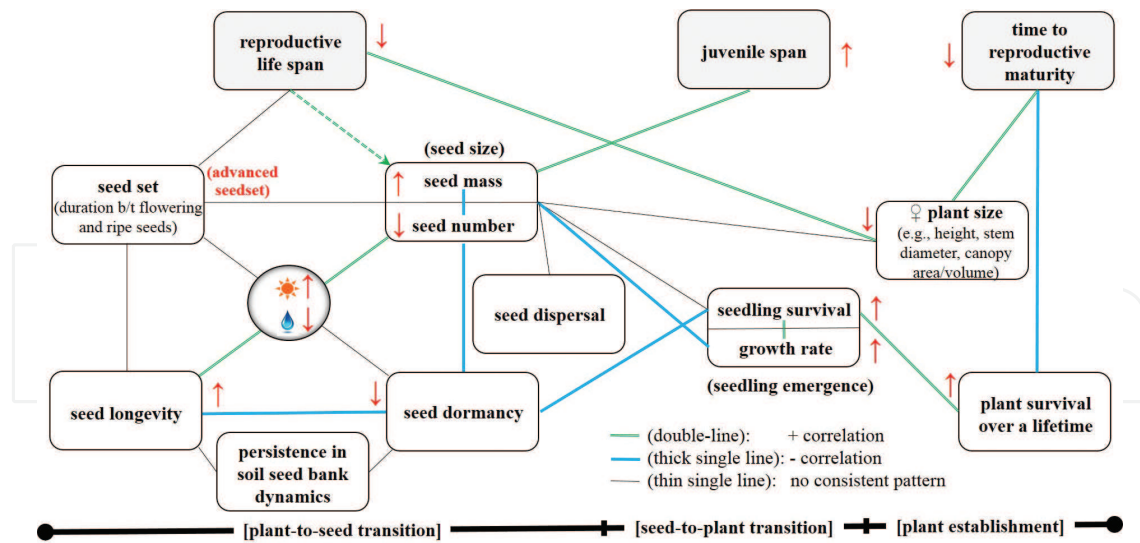


Figure 1. Relatedness among life-history and functional traits and the impact of climate change on the variation (and evolution) of these traits. Note: Lines give interactions between traits (boxes) in a positive or negative manner and the change of direction (↑ or ↓) depends on another trait(s). The arrow linking two traits prompts which trait affects the other. Sun and water drop symbols stand for temperature and rainfall, respectively.

Altered environment (♀)	Affected traits in offspring	Test species	References
Temperature (high or low)	Seed production, seed mass, flowering time	<i>Arabidopsis thaliana</i> , <i>Plantago lanceolata</i>	[162–164]
Light (shade or over-exposure)	Seed provisioning, seed mass, germination, seedling survival, biomass, life-history schedule	<i>Polygonum hydropiper</i> , <i>Campanulastrum americanum</i>	[165, 166]
Rainfall (drought)	Flowering (select for early flowering and short life cycles), seed provisioning, germination	<i>Brassica rapa</i> , <i>Polygonum persicaria</i>	[167–170]
Seasonal environments	Germination timing, life-history schedule	<i>Arabidopsis thaliana</i>	[74]
Salinity (high)	Germination, seedling growth	<i>Arabidopsis thaliana</i>	[171]
Nutrient (deficiency)	Plant height, biomass	<i>Oryza sativa</i>	[172]
Herbivory	Seed mass, germination, seedling growth, flowering, plant height, biomass	<i>Raphanus raphanistrum</i> , <i>Impatiens capensis</i>	[137, 138, 173]

Note: When maternal plants are deprived of resources, seed provisioning may be reduced (e.g., [145]), maintained or even increased (e.g., [167, 168, 174]), as trade-offs may exist between increased seed provisioning and decreased persistence in the soil seed bank [145, 167, 174] and thus the benefits may depend on a specific ecological setting.

Progressive global warming leads to widespread shifts toward earlier initiation of flowering in many plant populations, which contributes to an increase in the length of the flowering season in regions where flowering is temperature-dependent [175–177]. Note that longer growing seasons select for later flowering and thus warming and growing season may comprise a trade-off. As the detection of the relatedness between flowering locus and ambient temperature [72, 178], the flowering time diversity is associated with *cis*-regulatory variation [179] and further, flowering time loci restrict potential range size and niche breadth [180].

Table 2. Examples for the effect of different parental environments on offspring adaptive traits.

Last, we provided a summary of interplay patterns between traits (life-history, functional traits, and a combination thereof) as influenced by climatic factors in **Table 1** and **Figure 1**. We also listed examples on adaptive traits with transgenerational plasticity as responses to altered maternal environmental conditions in **Table 2**.

2. Life-history traits and their trade-offs

2.1. Seed size

The reproductive output of an organism is a critical life-history trait defining its fitness and is the result of both offspring number and quality. Seeds are time capsules and receptacles of life and seed mass is a crucial life-history trait that links the ecology of reproduction and seedling establishment with that of vegetative growth. Seed mass commonly varies over 11.5 orders of magnitude among coexisting plant species [31], while within-species variation in seed mass is typically in the range of two- to fourfold [32]. Extant flowering plants exhibit a wider range of seed sizes than nonflowering seed plants, and in particular, some of them can bear very small seeds [31]. Seed mass variation is a type of heteromorphism, which represents a classic trade-off. Production of dimorphic or heteromorphic seeds by a single plant allows plants to decrease temporal variance in offspring success through bet-hedging [i.e., a strategy that reduced temporal variance in fitness at the expense of a lowered arithmetic mean fitness] [33–35], or rather, a blend of plasticity [i.e., a capacity of a genotype to produce different phenotypes when exposed to different environmental conditions] and bet-hedging [36]. Heteromorphism enables a fraction of propagules to adapt to any given environment and may increase long-term reproductive success by reducing the risk of extinction, but it comes at the cost of decreasing immediate fitness [37].

Seed mass is closely correlated with changes in plant form and vegetative type, followed by spatial dispersal syndrome and net primary productivity [27, 38, 39]. Besides, latitude, genome size, forest structure, and life history all have been linked to seed size variation [40–43]. Effects of temperature on seed mass are not consistent, as both increased [44, 45] or decreased [46] seed masses have been documented. Seed mass variation within species is largely related to seed position within pods and fruits [47–49] and upper grains in the spikelet tend to be larger than bottom ones [50]. This is possibly due to physiological or morphological constraints on optimum resource allocation to seeds. The diversity of seed mass may be maintained by tolerance-fecundity trade-offs (i.e., more tolerant (fecund) species gain more (less) stressful regeneration sites, respectively) [51].

Empirical evidence favors the notion that seed production during mast years (i.e., good-seed years) is tightly related to high temperature in the previous spring and summer, late spring frost and summer rainfall of the last two years. The difference in temperature from one growing season to the next effectively predicted the occurrence of mast years [52–54]. Considering yearly climatic variability, Kelly et al. [55] developed a model based on temperature differentials over multiple seasons to predict seed yield [55] and this model was further validated by

Pearse et al. [56]. The robustness of these models is emanated from the hypothesized correlation between seed mass and the environment and, in turn, lends support to the crucial role of climate in seed mass modulations.

From a genetic perspective, seed mass and number can evolve independently. Both traits are affected by a large number of mostly non-overlapping quantitative trait loci (QTLs) in their genetic architecture, which has been manifested by using mapping lines created by two [57–60] and multiple parents [61]. This indicates that the relatedness between seed mass and number may not be invariably direct.

2.2. Seed dispersal in time and space

While seed dormancy is a means to disperse in time, seed dispersal is an important way to disperse in space (hereafter simply referred to as dispersal) and also a risk-spreading strategy [62, 63]. Selection in heterogeneous or unpredictable environments may favor plants to synchronize seed dispersal with environmental conditions allowing or deferring germination until suitable conditions occur [64]. As risk-reducing strategies, can seed dormancy and dispersal substitute for one another so that selection for one may weaken selection for the other? Theoretical expectations support such a trade-off or a negative covariation (reviewed in [62]), but empirical evidence is inconsistent (there are reports on complicated patterns or no relationship, e.g., [65]).

2.2.1. Seed dormancy

Seed dormancy is an innate constraint on germination timing under conditions that would otherwise promote germination in nondormant seeds [66] and prevent germination during periods that are ephemerally favorable [67]. Dormancy is significantly higher in annuals than in perennials (note that perenniality is an alternative risk-reducing strategy; [68]) and dormant seed banks are thus better associated with annuals than perennials [13, 25, 69]. Dormancy is an important adaptive trait that links plant life-history to seasonal change. Dormancy exists as a continuum with multiple layers (blocks to germination completion) that are successively taken off by appropriate environmental signals. These signals inform the seed whether it is in an appropriate habitat and time of the year suitable for the resulting plant to survive and reproduce. Seed germination timing is the earliest trait in plant life-history, which allows plants to regulate when and where they grow. It affects the evolution of other life-history traits that follow in the life cycle, such as fecundity and survival [70]. As such, seed dormancy may be construed as an adaptive strategy for survival during bad seasons and can exert cascading selective pressures on subsequent life stages.

Seeds temporarily block germination through adaptation to the prevailing environments so that germination is timed to avoid unfavorable environmental conditions for subsequent plant establishment and growth and therefore sets the context for the traits that follow [71]. Dormancy levels are maternally manipulated [72, 73] and determined by maternal responses to day length and temperature in many species [6, 74, 75]. Notably, induction of primary dormancy was greatly influenced by the effect of maternal environments on embryo/endosperm

[74, 76, 77] and/or on seed coat properties [78]. Dormancy intensity can be manipulated via controlling the daily circadian clock at reproduction [79]. Such effects can be passed down for multiple generations [80, 81] and have been observed even in long-lived perennials, such as conifers [82]. Dormancy manipulation involves dormancy-specific genomic imprinting programs that mainly occur in mature endosperm [83]. Owing to the similar functionality between plant seed endosperm and mammalian placenta, the kinship or parental conflict theory is often proposed to account for the evolutionary origin of imprinting [84].

Plants distribute their offspring across time, hedging their bets against unpredictable environments [37, 85]. This increases the likelihood that some seeds will survive regardless of environmental perturbations. Seed dormancy variability among individuals is associated with environmental heterogeneity [86] and heterogeneous environments may select for bet-hedging strategies, as population growth is an inherently multiplicative process that is very sensitive to occasionally extreme values [87]. Cohen indicated that low germination probabilities can be expected in harsh environments as individuals can germinate in improved conditions and decrease their average mortality [88]. However, Ellner predicted that increasing the frequency of favorable years may also lead to lower germination rates due to increased density-dependent effects imposed by competitive interactions [89, 90].

Based on mathematical modeling, large nondormant seeds would be selected for under constant unfavorable environments, whereas in temporally unpredictable environments, dormant seeds would be selected for, and their size would rely on the likelihood of predation of large seeds [91]. This alludes to the adaptive value of dormancy that may depend on the variability of the environment and the probability of survival of large seeds in the soil seed bank. Nondormant seeds in legumes can only evolve in climates with long growing seasons and/or in lineages that produce larger seeds; conversely, dormancy should be evolutionarily stable in temperate lineages with small seeds [92]. In light of this, it may be reasonable to extrapolate that, within a given lineage, taxa producing larger, nondormant seeds necessarily predominate in aseasonal environments, while plants bearing small, dormant seeds are dominant under short growing seasons [92].

2.2.2. *Seed dispersal syndrome*

Spatial aspects are especially important in the global climate change context, as temperature shifts depend on latitude and altitude gradients and species dispersal to higher altitudes and latitudes is thought to be a major constraint to their future survival. The evolution of local adaptation requires low dispersal (and selection against genotypes adapted to other localities) [93]. Also, spatial context influences gene flow and evolutionary dynamics with, again, important consequences for species competition and survival [94]. Differences in dispersal syndrome are likely to affect the shape of the dispersal kernel and the type of environments to which seeds are dispersed [95, 96]. On the one hand, they may evolve as phenotypic plasticity (e.g., bet-hedging) [97–99] in responses to selective factors, including reducing parent-offspring conflict or kin competition, the temporal heterogeneity of the environment, such as local population extinction [100–102] and avoiding inbreeding depression due to mating between related individuals (for dispersal only; [103]). Hence, seed dispersal promotes

adaptation, stability, and persistence [104]. On the other hand, various costs of dispersal have been postulated in theoretical models [such as fleshy fruits dispersed by animals [105], getting lost during displacements, dispersing in fragmented habitats [106], etc.], which end up concluding that increasing the cost of dispersal (certain selective forces) selects for lower dispersal [107]. Collectively, selection acts on trade-offs in temporal and spatial dispersal and eventually maximizes fitness [62]. These trade-offs can, in turn, introduce patterns of covariation among functional and life-history traits that correlate with dispersal (reviewed in [108]).

Further, dispersal syndrome is a consistent predictor of seed size especially in nonflowering seed plant groups [109]. In conifers (serotiny), seeds are generally larger in animal- than wind-dispersed species [110, 111]. This is in alignment with our intuition, because animals should be attracted to large, copious seeds and can be better than wind to disperse large propagules [112–114]. Moreover, spatial differences at the levels of environmental stochasticity, restricted dispersal, increased fragmentation, and intermediate survival during dormancy favor the adaptive diversification of bet-hedging dormancy strategies [115] and spatial heterogeneity and restricted dispersal are essential for evolutionary branching of germination strategies [116]. This suggests that dispersal and above-ground environmental fluctuations have a significant effect on the development of dormancy or germination polymorphisms.

2.3. Trade-offs among multiple life-history traits via stabilizing selection: a compromised strategy to recoup the disadvantage of respective traits

The Smith-Fretwell theory (1974) modeled the optimal seed mass and formalized the concept of a trade-off between producing a few, well provisioned offspring versus producing many poorly nourished individuals. It considers the offspring's lifetime fitness, given the population is stable during their life time. The role of differential seed mass in promoting species coexistence has been stressed in previous theoretical studies [117–119]. Evolution of seed mass results in the fixation of a given strategy and evolved seed mass decreases when seed dormancy is lowered [120]. Large seed mass, on the one hand, confers direct advantages to many fitness-related plant characteristics, including recruitment and survivorship [121, 122] and establishment [32, 122], because large seeds accumulate copious nourishing substances for germination and have better tolerance in face of disturbances (e.g., abiotic stresses) [119, 123]. Furthermore, for a given reproductive investment, seed mass is negatively correlated with seed number [124–126] and large seeds are less dispersible due to their great mass [127]. However, can the survival advantage of large-seeded species really counterbalance the greater seed yield of small-seeded species?

The advantage of large-seededness is generally temporary, probably expiring when all maternal reserves have been deployed [123]. This means large-seeded species have a survival advantage over small-seeded species solely during early seedling establishment [122]. Actually, there is no or even weak negative correlation between seed mass and overall seedling survival [122, 123]. Because slow growth rate (due to slow metabolic rate) increases the capability of persistence under stress and the duration of exposure to juvenile mortality. Greater survival per unit time associated with large-seeded species may be canceled out by the longer time to maturity.

Here, we speculate possible impacts of elements of plant strategy systems (e.g., vegetative functional traits) on seed ecology. Larger plant size has higher annual photosynthetic incomes, giving the plant more energy to allocate to seed production (increased seed number, heavier mass, or a trade-off between the two). A species with a large adult stature will necessarily have a lengthy juvenile period to produce large, well-provisioned offspring, which makes up for a high rate of juvenile mortality. By contrast, smaller plant size of small-seeded species may have less photosynthate to allocate to reproduction. Further, they also tend to have shorter reproductive life span (i.e., less total investment to offspring and lower mortality). Less input from maternal plants further erodes the apparent advantage that small-seeded species harbor during seed production.

In addition to seed dormancy and dispersal, there are other risk-spreading strategies. For instance, there is a negative trade-off between dormancy and longevity (a survival strategy) to reduce risk of reproductive failures in time [69, 128, 129]. Iteroparous (i.e., reproducing more than once in a lifetime) perennial plants increase their probability of encountering favorable conditions for reproduction in time [130–132]. Therefore, the need for seed dormancy in perennials may be negated and perenniality may select against seed dormancy [128, 129].

Additionally, it is reported that dormancy is also dependent on the likelihood of seed predation and nondormancy may evolve as part of a predator avoidance strategy [133, 134] and also with the involvement of environmental pressures [135]. The risk of predation is thought to be proportional to seed size due to its detectability and nutritious contents. However, such risk is lower in large than small seeds, possibly because size is positively correlated with defense mechanisms [136]. Furthermore, maternal herbivory has a major impact on seed size [137, 138] (also see **Table 2**; mediated by phytohormone signaling pathways that affect seed filling [e.g., gibberellins, auxin, brassinosteroid] [139, 140]) and dormancy [141] (mediated by jasmonate signaling pathway and resultant changes in the sensitivity of seed germination to ABA). Thus, whether dormancy or nondormancy is favored by selection ultimately depends on seed size [92].

In a nutshell, there is no prevalent relationship between seed mass and number, in the sense that the advantages that small-seeded species gain during seed production must be counterbalanced somewhere else in the life cycle and seed number is just one of the possibilities to make up the loss of small seededness. Seed mass is determined via a process of stabilizing selection, which may operate through selections on trade-offs among seedling survival, dormancy, dispersal, seed number, and predation [142], and may play a central role among a correlated suite of traits that covaries across a spectrum of life-history strategies.

3. Conclusions

This chapter intends to direct readers' attention to consider multiple life-history traits in the life cycle when studying plant life-history evolution, as selection for one strategy (not necessarily limited to one single trait) may constrain another. Disentangling the trade-offs of how

disadvantages in one studied trait may be made up by being an advantage in another trait(s) helps essentially understand the evolution of a particular trait. Moreover, these trade-offs are essential for understanding the complex response of species to climate change.

Author details

Yang Liu^{1*}, Jeffrey L. Walck^{2*} and Yousry A. El-Kassaby^{1*}

*Address all correspondence to: yang.liu@ubc.ca, Jeffrey.Walck@mtsu.edu and y.el-kassaby@ubc.ca

1 Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, BC, Canada

2 Department of Biology, Middle Tennessee State University, Murfreesboro, TN, USA

References

- [1] Calow P. The Encyclopedia of Ecology and Environmental Management. New York: Blackwell Science; 1998
- [2] Moles AT, Westoby M. Latitude, seed predation and seed mass. *Journal of Biogeography*. 2003;**30**(1):105-128
- [3] Morin X, Chuine I. Niche breadth, competitive strength and range size of tree species: A trade-off based framework to understand species distribution. *Ecology Letters*. 2006;**9**(2):185-195
- [4] Baskin CC, Baskin JM. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. 2nd ed. San Diego, California: Academic Press; 2014. p. 666
- [5] Vidigal DS, Marques AC, Willems LA, Buijs G, Méndez-Vigo B, Hilhorst HW, et al. Altitudinal and climatic associations of seed dormancy and flowering traits evidence adaptation of annual life cycle timing in *Arabidopsis thaliana*. *Plant, Cell & Environment*. 2016;**39**(8):1737-1748
- [6] Fenner M. The effects of the parent environment on seed germinability. *Seed Science Research*. 1991;**1**:75-84
- [7] Huang ZY, Footitt S, Finch-Savage WE. The effect of temperature on reproduction in the summer and winter annual *Arabidopsis thaliana* ecotypes Bur and Cvi. *Annals of Botany*. 2014;**113**(6):921-929
- [8] Springthorpe V, Penfield S. Flowering time and seed dormancy control use external coincidence to generate life history strategy. *eLIFE*. 2015;**4**:e05557
- [9] Schmutz H, Bachmann K, Weber WE, Horres R, Hoffmann MH. Effects of preconditioning and temperature during germination of 73 natural accessions of *Arabidopsis thaliana*. *Annals of Botany*. 2006;**97**(4):623-634

- [10] Burghardt LT, Edwards BR, Donohue K. Multiple paths to similar germination behavior in *Arabidopsis thaliana*. *New Phytologist*. 2016;**209**(3):1301-1312
- [11] Thompson K, Grime JP. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*. 1979;**67**(3):893-921
- [12] Grime JP, Mason G, Curtis AV, Rodman J, Band SR, Mowforth MAG, et al. A comparative study of germination characteristics in a local flora. *Journal of Ecology*. 1981;**69**(3):1017-1059
- [13] Rees M. Evolutionary ecology of seed dormancy and seed size. *Philosophical Transactions of the Royal Society B*. 1996;**351**(1345):1299-1308
- [14] Kiviniemi K. Evolution of recruitment features in plants: A comparative study of species in the Rosaceae. *Oikos*. 2001;**94**(2):250-262
- [15] Larios E, Búrquez A, Becerra JX, Venable DL. Natural selection on seed size through the life cycle of a desert annual plant. *Ecology*. 2014;**95**(11):3213-3220
- [16] Parsons RF. Incidence and ecology of very fast germination. *Seed Science Research*. 2012;**22**(3):161-167
- [17] Vandeloos F, Janssens SB, Probert RJ. Relative embryo length as an adaptation to habitat and life cycle in Apiaceae. *New Phytologist*. 2012;**195**(2):479-487
- [18] Debieu M, Tang C, Stich B, Sikosek T, Effgen S, Josephs E, et al. Co-variation between seed dormancy, growth rate and flowering time changes with latitude in *Arabidopsis thaliana*. *PloS One*. 2013;**8**(5):e61075
- [19] Jurik TW, Wang SC, Vandervalk AG. Effects of sediment load on seedling emergence from wetland seed banks. *Wetlands*. 1994;**14**(3):159-165
- [20] Maun MA, Lapierre J. Effects of burial by sand on seed germination and seedling emergence of four dune species. *American Journal of Botany*. 1986;**73**(3):450-455
- [21] Pearson TRH, Burslem DFRP, Mullins CE, Dalling JW. Germination ecology of neotropical pioneers: Interacting effects of environmental conditions and seed size. *Ecology*. 2002;**83**(10):2798-2807
- [22] Ghera CM, Arnold RLB, Martinezghera MA. The role of fluctuating temperatures in germination and establishment of *Sorghum halepense* – Regulation of germination at increasing depths. *Functional Ecology*. 1992;**6**(4):460-468
- [23] Xia Q, Ando M, Seiwa K. Interaction of seed size with light quality and temperature regimes as germination cues in 10 temperate pioneer tree species. *Functional Ecology*. 2016;**30**(6):866-874
- [24] Nguyen TP, Keizer P, van Eeuwijk F, Smeekens S, Bentsink L. Natural variation for seed longevity and seed dormancy are negatively correlated in *Arabidopsis*. *Plant Physiology*. 2012;**160**(4):2083-2092
- [25] Thompson K, Bakker JP, Bekker RM, Hodgson JG. Ecological correlates of seed persistence in soil in the north-west European flora. *Journal of Ecology*. 1998;**86**:163-169

- [26] Leishman MR, Westoby M, Jurado E. Correlates of seed size variation: A comparison among five temperate floras. *Journal of Ecology*. 1995;**83**:517-529
- [27] Moles AT, Ackerly DD, Webb CO, Tweddle JC, Dickie JB, Pitman AJ, et al. Factors that shape seed mass evolution. *Proceedings of the National Academy of Sciences of the United States of America*. 2005;**102**(30):10540-10544
- [28] Moles AT, Ackerly DD, Webb CO, Tweddle JC, Dickie JB, Westoby M. Response to comment on "A brief history of seed size". *Science*. 2005;**310**(5749):783
- [29] Westoby M. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*. 1998;**199**(2):213-227
- [30] Hoyle GL, Steadman KJ, Good RB, McIntosh EJ, Galea LME, Nicotra AB. Seed germination strategies: An evolutionary trajectory independent of vegetative functional traits. *Frontiers in Plant Science*. 2015;**6**:731
- [31] Moles AT, Ackerly DD, Webb CO, Tweddle JC, Dickie JB, Westoby M. A brief history of seed size. *Science*. 2005;**307**(5709):576-580
- [32] Leishman MR, Wright IJ, Moles AT, Westoby M. Seeds: The ecology of regeneration in plant communities. In: Fenner M, editor. *The Evolutionary Ecology of Seed Size*. New York: Oxford University Press; 2000
- [33] Venable DL, Búrquez A, Corral G, Morales E, Espinosa F. The ecology of seed heteromorphism in *Heterosperma pinnatum* in central Mexico. *Ecology*. 1987;**68**:65-76
- [34] Baskin JM, Lu JJ, Baskin CC, Tan DY, Wang L. Diaspore dispersal ability and degree of dormancy in heteromorphic species of cold deserts of northwest China: A review. *Perspectives in Plant Ecology Evolution and Systematics*. 2014;**16**(2):93-99
- [35] Imbert E. Ecological consequences and ontogeny of seed heteromorphism. *Perspectives in Plant Ecology Evolution and Systematics*. 2002;**5**(1):13-36
- [36] Lenser T, Graeber K, Cevik ÖS, Adigüzel N, Dönmez AA, Grosche C, et al. Developmental control and plasticity of fruit and seed dimorphism in *Aethionema arabicum*. *Plant Physiology*. 2016;**172**(3):1691-1707
- [37] Venable DL. Bet hedging in a guild of desert annuals. *Ecology*. 2007;**88**(5):1086-1090
- [38] Moles AT, Ackerly DD, Tweddle JC, Dickie JB, Smith R, Leishman MR, et al. Global patterns in seed size. *Global Ecology and Biogeography*. 2007;**16**(1):109-116
- [39] Díaz S, Kattge J, Cornelissen JH, Wright IJ, Lavorel S, Dray S, et al. The global spectrum of plant form and function. *Nature*. 2016;**529**(7585):167-171
- [40] Salisbury E. Seed size and mass in relation to environment. *Proceedings of the Royal Society Series B-Biological Sciences*. 1974;**186**(1083):83-88
- [41] Lord J, Egan J, Clifford T, Jurado E, Leishman M, Williams D, et al. Larger seeds in tropical floras: Consistent patterns independent of growth form and dispersal mode. *Journal of Biogeography*. 1997;**24**(2):205-211

- [42] Beaulieu JM, Moles AT, Leitch IJ, Bennett MD, Dickie JB, Knight CA. Correlated evolution of genome size and seed mass. *New Phytologist*. 2007;**173**(2):422-437
- [43] Rueda M, Godoy O, Hawkins BA. Spatial and evolutionary parallelism between shade and drought tolerance explains the distributions of conifers in the conterminous United States. *Global Ecology and Biogeography*. 2017;**26**(1):31-42
- [44] Murray BR, Brown AHD, Dickman CR, Crowther MS. Geographical gradients in seed mass in relation to climate. *Journal of Biogeography*. 2004;**31**(3):379-388
- [45] Liu Y, Wang T, El-Kassaby YA. Contributions of dynamic environmental signals during life-cycle transitions to early life-history traits in lodgepole pine (*Pinus contorta* Dougl.). *Biogeosciences*. 2016;**13**:2945-2958
- [46] Hovenden MJ, Wills KE, Chaplin RE, Vander Schoor JK, Williams AL, Osanai YUI, et al. Warming and elevated CO₂ affect the relationship between seed mass, germinability and seedling growth in *Austrodanthonia caespitosa*, a dominant Australian grass. *Global Change Biology*. 2008;**14**(7):1633-1641
- [47] Wulff RD. Seed size variation in *Desmodium Paniculatum*. I. Factors affecting seed size. *Journal of Ecology*. 1986;**74**(1):87-97
- [48] Michaels HJ, Benner B, Hartgerink AP, Lee TD, Rice S, Willson MF, et al. Seed size variation: Magnitude, distribution, and ecological correlates. *Evolutionary Ecology*. 1988;**2**(2):157-166
- [49] Obeso JR. Seed mass variation in the perennial herb *Asphodelus albus*: Sources of variation and position effect. *Oecologia*. 1993;**93**(4):571-575
- [50] Volis S. Seed heteromorphism in *Triticum dicoccoides*: Association between seed positions within a dispersal unit and dormancy. *Oecologia*. 2016;**181**(2):401-412
- [51] Muller-Landau HC. The tolerance-fecundity trade-off and the maintenance of diversity in seed size. *Proceedings of the National Academy of Sciences of the United States of America*. 2010;**107**(9):4242-4247
- [52] Schauber EM, Kelly D, Turchin P, Simon C, Lee WG, Allen RB, et al. Masting by eighteen New Zealand plant species: The role of temperature as a synchronizing cue. *Ecology*. 2002;**83**(5):1214-1225
- [53] Smajll SJ, Clinton PW, Allen RB, Davis MR. Climate cues and resources interact to determine seed production by a masting species. *Journal of Ecology*. 2011;**99**(3):870-877
- [54] Krebs CJ, LaMontagne JM, Kenney AJ, Boutin S. Climatic determinants of white spruce cone crops in the boreal forest of southwestern Yukon. *Botany*. 2012;**90**(2):113-119
- [55] Kelly D, Geldenhuis A, James A, Penelope Holland E, Plank MJ, Brockie RE, et al. Of mast and mean: Differential-temperature cue makes mast seeding insensitive to climate change. *Ecology Letters*. 2013;**16**(1):90-98

- [56] Pearse IS, Koenig WD, Knops JMH. Cues versus proximate drivers: Testing the mechanism behind masting behavior. *Oikos*. 2014;**123**(2):179-184
- [57] Alonso-Blanco C, Blankestijn-de Vries H, Hanhart CJ, Koornneef M. Natural allelic variation at seed size loci in relation to other life history traits of *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences of the United States of America*. 1999;**96**(8):4710-4717
- [58] Moore CR, Gronwall DS, Miller ND, Spalding EP. Mapping quantitative trait loci affecting *Arabidopsis thaliana* seed morphology features extracted computationally from images. *G3-Genes Genomes Genetics*. 2013;**3**(1):109-118
- [59] Herridge RP, Day RC, Baldwin S, Macknight RC. Rapid analysis of seed size in *Arabidopsis* for mutant and QTL discovery. *Plant Methods*. 2011;**7**(1):3
- [60] Van Daele I, Gonzalez N, Vercauteren I, de Smet L, Inzé D, Roldán-Ruiz I, et al. A comparative study of seed yield parameters in *Arabidopsis thaliana* mutants and transgenics. *Plant Biotechnology Journal*. 2012;**10**(4):488-500
- [61] Gnan S, Priest A, Kover PX. The genetic basis of natural variation in seed size and seed number and their trade-off using *Arabidopsis thaliana* MAGIC Lines. *Genetics*. 2014;**198**(4):1751-1758
- [62] Buoro M, Carlson SM. Life-history syndromes: Integrating dispersal through space and time. *Ecology Letters*. 2014;**17**(6):756-767
- [63] Cohen D, Levin SA. The interaction between dispersal and dormancy strategies in varying and heterogeneous environments. In: Teramoto E, Yamaguti M, editors. *Mathematical Topics in Population Biology, Morphogenesis and Neurosciences*. Vol. 71. Heidelberg: Springer-Verlag; 1987. pp. 110-122
- [64] Freas KM, Kemp PR. Some relationships between environmental reliability and seed dormancy in desert annual plants. *Journal of Ecology*. 1983;**71**:211-217
- [65] Siewert W, Tielbörger K. Dispersal-dormancy relationships in annual plants: Putting model predictions to the test. *American Naturalist*. 2010;**176**(4):490-500
- [66] Simpson G. *Seed Dormancy in Grasses*. Cambridge, UK: Cambridge University Press; 1990
- [67] Bewley JD. Seed germination and dormancy. *Plant Cell*. 1997;**9**(7):1055-1066
- [68] de Waal C, Anderson B, Ellis AG. Dispersal, dormancy and life-history tradeoffs at the individual, population and species levels in southern African Asteraceae. *New Phytologist*. 2016;**210**(1):356-365
- [69] Rees M. Trade-offs among dispersal strategies in British plants. *Nature*. 1993;**366**(6451):150-152
- [70] Hamilton WD. The moulding of senescence by natural selection. *Journal of Theoretical Biology*. 1966;**12**:12-45

- [71] Donohue K, de Casas RR, Burghardt L, Kovach K, Willis CG. Germination, postgermination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics*. 2010;**41**:293-319
- [72] Chen M, MacGregor DR, Dave A, Florance H, Moore K, Paszkiewicz K, et al. Maternal temperature history activates Flowering Locus T in fruits to control progeny dormancy according to time of year. *Proceedings of the National Academy of Sciences of the United States of America*. 2014;**111**:18787-18792
- [73] Chiang GCK, Barua D, Kramer EM, Amasino RM, Donohue K. Major flowering time gene, *FLOWERING LOCUS C*, regulates seed germination in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences of the United States of America*. 2009;**106**(28):11661-11666
- [74] Donohue K. Completing the cycle: Maternal effects as the missing link in plant life histories. *Philosophical Transactions of the Royal Society B*. 2009;**364**(1520):1059-1074
- [75] Kendall S, Penfield S. Maternal and zygotic temperature signalling in the control of seed dormancy and germination. *Seed Science Research*. 2012;**22**:S23–S29
- [76] Schmitt J, Niles J, Wulff R. Norms of reaction of seed traits to maternal environments in *Plantago lanceolata*. *American Naturalist*. 1992;**139**(3):451-466
- [77] Postma FM, Ågren J. Maternal environment affects the genetic basis of seed dormancy in *Arabidopsis thaliana*. *Molecular Ecology*. 2015;**24**(4):785-797
- [78] MacGregor DR, Kendall SL, Florance H, Fedi F, Moore K, Paszkiewicz K, et al. Seed production temperature regulation of primary dormancy occurs through control of seed coat phenylpropanoid metabolism. *New Phytologist*. 2015;**205**(2):642-652
- [79] Footitt S, Ölcer-Footitt H, Hambidge AJ, Finch-Savage WE. A laboratory simulation of *Arabidopsis* seed dormancy cycling provides new insight into its regulation by clock genes and the dormancy-related genes *DOG1*, *MFT*, *CIPK23* and *PHYA*. *Plant, Cell & Environment*. 2017 (in press)
- [80] Lu JJ, Tan DY, Baskin CC, Baskin JM. Effects of germination season on life history traits and on transgenerational plasticity in seed dormancy in a cold desert annual. *Scientific Reports*. 2016;**6**:25076
- [81] Galloway LF, Etterson JR. Transgenerational plasticity is adaptive in the wild. *Science*. 2007;**318**(5853):1134-1136
- [82] Stoehr MU, L'Hirondelle SJ, Binder WD, Webber JE. Parental environment after effects on germination, growth, and adaptive traits in selected white spruce families. *Canadian Journal of Forest Research*. 1998;**28**(3):418-426
- [83] Piskurewicz U, Iwasaki M, Susaki D, Megies C, Kinoshita T, Lopez-Molina L. Dormancy-specific imprinting underlies maternal inheritance of seed dormancy in *Arabidopsis thaliana*. *eLIFE*. 2016;**5**:e19573

- [84] Haig D, Westoby M. Parent-specific gene expression and the triploid endosperm. *American Naturalist*. 1989;**134**(1):147-155
- [85] Poisot T, Bever JD, Nemri A, Thrall PH, Hochberg ME. A conceptual framework for the evolution of ecological specialisation. *Ecology Letters*. 2011;**14**(9):841-851
- [86] Angevine MW, Chabot BF. Seed germination syndromes in higher plants. In: Solbrig OT, Jain S, Johnson GB, Raven PH, editors. *Topics in plant population biology*. New York, NY: Columbia University Press; 1979
- [87] Dempster ER. Maintenance of genetic heterogeneity. *Cold Spring Harbor Symposia on Quantitative Biology*. 1955;**20**:25-32
- [88] Cohen D. Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology*. 1966;**12**(1):119-129
- [89] Ellner S. ESS germination strategies in randomly varying environments. I. Logistic-type models. *Theoretical Population Biology*. 1985;**28**(1):50-79
- [90] Ellner S. ESS germination strategies in randomly varying environments. II. Reciprocal yield-law models. *Theoretical Population Biology*. 1985;**28**(1):80-116
- [91] Volis S, Bohrer G. Joint evolution of seed traits along an aridity gradient: Seed size and dormancy are not two substitutable evolutionary traits in temporally heterogeneous environment. *New Phytologist*. 2013;**197**(2):655-667
- [92] Rubio de Casas R, Willis CG, Pearse WD, Baskin CC, Baskin JM, Cavender-Bares J. Global biogeography of seed dormancy is determined by seasonality and seed size: A case study in the legumes. *New Phytologist*. 2017 (in press)
- [93] Kawecki TJ, Ebert D. Conceptual issues in local adaptation. *Ecology Letters*. 2004;**7**(12):1225-1241
- [94] Norberg J, Urban MC, Vellend M, Klausmeier CA, Loeuille N. Eco-evolutionary responses of biodiversity to climate change. *Nature Climate Change*. 2012;**2**(10):747-751
- [95] Garcia-Castaño JL, Kollmann J, Jordano P. Spatial variation of post-dispersal seed removal by rodents in highland microhabitats of Spain and Switzerland. *Seed Science and Technology*. 2006;**16**(3):213-222
- [96] Russo SE, Portnoy S, Augspurger CK. Incorporating animal behavior into seed dispersal models: Implications for seed shadows. *Ecology*. 2006;**87**(12):3160-3174
- [97] Slatkin M. Hedging ones evolutionary bets. *Nature*. 1974;**250**:704-705
- [98] Gomez-Mestre I, Jovani R. A heuristic model on the role of plasticity in adaptive evolution: Plasticity increases adaptation, population viability and genetic variation. *Proceedings of the Royal Society B: Biological Sciences*. 2013;**280**(1771):20131869
- [99] Philippi T, Seger J. Hedging one's evolutionary bets, revisited. *Trends in Ecology & Evolution*. 1989;**4**(2):41-44
- [100] Ellner S. Germination dimorphisms and parent offspring conflict in seed germination. *Journal of Theoretical Biology*. 1986;**123**(2):173-185

- [101] Vitalis R, Rousset F, Kobayashi Y, Olivieri I, Gandon S. The joint evolution of dispersal and dormancy in a metapopulation with local extinctions and kin competition. *Evolution*. 2013;**67**(6):1676-1691
- [102] Gremer JR, Venable DL. Bet hedging in desert winter annual plants: Optimal germination strategies in a variable environment. *Ecology Letters*. 2014;**17**(3):380-387
- [103] Bengtsson BO. Avoiding inbreeding: At what cost? *Journal of Theoretical Biology*. 1978;**73**(3):439-444
- [104] Kovach-Orr C, Fussmann GF. Evolutionary and plastic rescue in multitrophic model communities. *Philosophical Transactions of the Royal Society B*. 2013;**368**(1610):20120084
- [105] Herrera CM. Plant-vertebrate seed dispersal systems in the Mediterranean: Ecological, evolutionary, and historical determinants. *Annual Review of Ecology and Systematics*. 1995;**26**:705-727
- [106] Cheptou PO, Carrue O, Rouifed S, Cantarel A. Rapid evolution of seed dispersal in an urban environment in the weed *Crepis sancta*. *Proceedings of the National Academy of Sciences of the United States of America*. 2008;**105**(10):3796-3799
- [107] Gandon S, Michalakis Y. Multiple causes of the evolution of dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. *Dispersal*. Oxford, New York: Oxford University Press; 2001
- [108] Ronce O, Clobert J. Dispersal syndromes. In: Clobert J, Baguette M, Benton TG, Bullock JM, Ducatez S, editors. *Dispersal ecology and evolution*. Oxford, UK: Oxford University Press; 2012
- [109] Leslie AB, Beaulieu JM, Mathews S. Variation in seed size is structured by dispersal syndrome and cone morphology in conifers and other nonflowering seed plants. *New Phytologist*. 2017 (in press)
- [110] Tomback DF, Linhart YB. The evolution of bird-dispersed pines. *Evolutionary Ecology*. 1990;**4**(3):185-219
- [111] Lanner RM. Seed dispersal in *Pinus*. In: Richardson DM, editor. *Ecology and Biogeography of Pinus*. Cambridge, UK: Cambridge University Press; 1998. pp. 281-295
- [112] Leishman MR, Westoby M. The role of seed size in seedling establishment in dry soil conditions – Experimental evidence from semiarid species. *Journal of Ecology*. 1994;**82**(2):249-258
- [113] Primack RB. Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics*. 1987;**18**:409-430
- [114] Hughes L, Dunlop M, French K, Leishman MR, Rice B, Rodgerson L, et al. Predicting dispersal spectra – A minimal set of hypotheses based on plant attributes. *Journal of Ecology*. 1994;**82**(4):933-950
- [115] Rajon E, Venner S, Menu F. Spatially heterogeneous stochasticity and the adaptive diversification of dormancy. *Journal of Evolutionary Biology*. 2009;**22**(10):2094-2103

- [116] Mathias A, Kisdi E. Adaptive diversification of germination strategies. *Proceedings of the Royal Society B: Biological Sciences*. 2002;**269**(1487):151-155
- [117] Geritz SAH. Evolutionarily stable seed polymorphism and small-scale spatial variation in seedling density. *American Naturalist*. 1995;**146**(5):685-707
- [118] Rees M, Westoby M. Game-theoretical evolution of seed mass in multi-species ecological models. *Oikos*. 1997;**78**(1):116-126
- [119] Geritz SA, van der Meijden E, Metz JA. Evolutionary dynamics of seed size and seedling competitive ability. *Theoretical Population Biology*. 1999;**55**(3):324-343
- [120] Liu Y, Barot S, El-Kassaby YA, Loeuille N. Impact of temperature shifts on the joint evolution of seed dormancy and size. *Ecology and Evolution*. 2017;**7**(1):26-37
- [121] McGinley MA, Temme DH, Geber MA. Parental investment in offspring in variable environments – Theoretical and empirical considerations. *American Naturalist*. 1987;**130**(3):370-398
- [122] Moles AT, Westoby M. Seedling survival and seed size: A synthesis of the literature. *Journal of Ecology*. 2004;**92**(3):372-383
- [123] Westoby M, Falster D, Moles A, Vesk P, Wright I. Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology Evolution and Systematics*. 2002;**33**:125-159
- [124] McGinley MA, Charnov EL. Multiple resources and the optimal balance between size and number of offspring. *Evolutionary Ecology*. 1988;**2**(1):77-84
- [125] Jakobsson A, Eriksson O. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos*. 2000;**88**:494-502
- [126] Harper JL, Lovell PH, Moore KG. The shapes and sizes of seeds. *Annual Review of Ecology and Systematics*. 1970;**1**:327-356
- [127] Salisbury E. The survival value of modes of dispersal. *Proceedings of the Royal Society B: Biological Sciences*. 1975;**188**:183-188
- [128] Rees M. Delayed germination of seeds: A look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. *American Naturalist*. 1994;**144**(1):43-64
- [129] Tuljapurkar S. Delayed reproduction and fitness in variable environments. *Proceedings of the National Academy of Sciences of the United States of America*. 1990;**87**(3):1139-1143
- [130] Bulmer MG. Selection for iteroparity in a variable environment. *American Naturalist*. 1985;**126**(1):63-71
- [131] Ehrlén J, van Groenendael JM. The trade-off between dispersability and longevity: An important aspect of plant species diversity. *Applied Vegetation Science*. 1998;**1**(1):29-36

- [132] Zeineddine M, Jansen VAA. To age, to die: Parity, evolutionary tracking and Cole's paradox. *Evolution*. 2009;**63**(6):1498-1507
- [133] Dalling JW, Davis AS, Schutte BJ, Arnold AE. Seed survival in soil: Interacting effects of predation, dormancy and the soil microbial community. *Journal of Ecology*. 2011;**99**(1):89-95
- [134] Paulsen TR, Colville L, Kranner I, Daws MI, Högstedt G, Vandvik V, et al. Physical dormancy in seeds: A game of hide and seek? *New Phytologist*. 2013;**198**(2):496-503
- [135] Jayasuriya KMG, Athugala YS, Wijayasinghe MM, Baskin JM, Baskin CC, Mahadevan N. The crypsis hypothesis: A stenopic view of the selective factors in the evolution of physical dormancy in seeds. *Seed Science Research*. 2015;**25**(2):127-137
- [136] Schutte BJ, Davis AS, Peinado SA, Ashigh J. Seed-coat thickness data clarify seed size-seed-bank persistence trade-offs in *Abutilon theophrasti* (Malvaceae). *Seed Science Research*. 2014;**24**(2):119-131
- [137] Agrawal AA. Transgenerational consequences of plant responses to herbivory: An adaptive maternal effect? *American Naturalist*. 2001;**157**(5):555-569
- [138] Agrawal AA, Laforsch C, Tollrian R. Transgenerational induction of defences in animals and plants. *Nature*. 1999;**401**(6748):60-63
- [139] Hu J, Mitchum MG, Barnaby N, Ayele BT, Ogawa M, Nam E, et al. Potential sites of bioactive gibberellin production during reproductive growth in *Arabidopsis*. *Plant Cell*. 2008;**20**(2):320-336
- [140] Li N, Li YH. Signaling pathways of seed size control in plants. *Current Opinion in Plant Biology*. 2016;**33**:23-32
- [141] Singh P, Dave A, Vaistij FE, Worrall D, Holroyd GH, Wells JG, et al. Jasmonic acid-dependent regulation of seed dormancy following maternal herbivory in *Arabidopsis*. *New Phytologist*. 2017 (in press)
- [142] Venable DL, Brown JS. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *American Naturalist*. 1988;**131**:360-384
- [143] Thompson K, Ceriani RM, Bakker JP, Bekker RM. Are seed dormancy and persistence in soil related? *Seed Science Research*. 2003;**13**(2):97-100
- [144] Moles AT, Westoby M. Seed mass and seedling establishment after fire in Ku-ring-gai Chase National Park, Sydney, Australia. *Austral Ecology*. 2004;**29**(4):383-390
- [145] Fenner M, Thompson K. *The Ecology of Seeds*. Cambridge, UK: Cambridge University Press; 2005
- [146] Poorter L, Rose S. Light-dependent changes in the relationship between seed mass and seedling traits: A meta-analysis for rain forest tree species. *Oecologia*. 2005;**142**(3):378-387

- [147] Maranon T, Grubb PJ. Physiological basis and ecological significance of the seed size and relative growth rate relationship in Mediterranean annuals. *Functional Ecology*. 1993;**7**(5):591-599
- [148] Hendrix SD, Sun IF. Inter-and intraspecific variation in seed mass in seven species of umbellifer. *New Phytologist*. 1989;**112**:445-452
- [149] Stocklin J, Favre P. Effects of plant size and morphological constraints on variation in reproductive components in two related species of *Epilobium*. *Journal of Ecology*. 1994;**82**(4):735-746
- [150] Moles AT, Falster DS, Leishman MR, Westoby M. Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. *Journal of Ecology*. 2004;**92**(3):384-396
- [151] Willis CG, Baskin CC, Baskin JM, Auld JR, Venable DL, Cavender-Bares J, et al. The evolution of seed dormancy: Environmental cues, evolutionary hubs, and diversification of the seed plants. *New Phytologist*. 2014;**203**(1):300-309
- [152] Scott RJ, Spielman M, Bailey J, Dickinson HG. Parent-of-origin effects on seed development in *Arabidopsis thaliana*. *Development*. 1998;**125**(17):3329-3341
- [153] Lamont BB, Lemaitre DC, Cowling RM, Enright NJ. Canopy seed storage in woody plants. *Botanical Review*. 1991;**57**(4):277-317
- [154] Hoyle GL, Venn SE, Steadman KJ, Good RB, McAuliffe EJ, Williams ER, et al. Soil warming increases plant species richness but decreases germination from the alpine soil seed bank. *Global Change Biology*. 2013;**19**(5):1549-1561
- [155] Cochrane A, Holye G, Yates C, Wood J, Nicotra A. Climate warming delays and decreases seedling emergence in a Mediterranean ecosystem. *Oikos*. 2015;**124**(2):150-160
- [156] Childs DZ, Metcalf CJE, Rees M. Evolutionary bet-hedging in the real world: Empirical evidence and challenges revealed by plants. *Proceedings of the Royal Society B: Biological Sciences*. 2010;**277**(1697):3055-3064
- [157] Probert RJ. The role of temperature in the regulation of seed dormancy and germination. In: Fenner M, editor. *Seeds: The Ecology of Regeneration in Plant Communities*. Wallingford, Oxon: CABI; 2000. pp. 261-292
- [158] Ooi MKJ, Auld TD, Denham AJ. Climate change and bet-hedging: Interactions between increased soil temperatures and seed bank persistence. *Global Change Biology*. 2009;**15**:2375-2386
- [159] Evans ME, Dennehy JJ. Germ banking: Bet-hedging and variable release from egg and seed dormancy. *The Quarterly Review of Biology*. 2005;**80**(4):431-451
- [160] Walck JL, Hidayati SN, Dixon KW, Thompson K, Poschlod P. Climate change and plant regeneration from seed. *Global Change Biology*. 2011;**17**(6):2145-2161

- [161] Roach DA, Wulff RD. Maternal effects in plants. *Annual Review of Ecology*. 1987;**18**: 209-235
- [162] Whittle CA, Otto SP, Johnston MO, Krochko JE. Adaptive epigenetic memory of ancestral temperature regime in *Arabidopsis thaliana*. *Botany*. 2009;**87**(6):650-657
- [163] Case AL, Lacey EP, Hopkins RG. Parental effects in *Plantago lanceolata* L.II. Manipulation of grandparental temperature and parental flowering time. *Heredity*. 1996;**76**:287-295
- [164] Lacey EP. Parental effects in *Plantago lanceolata* L. I. A growth chamber experiment to examine pre- and postzygotic temperature effects. *Evolution*. 1996;**50**(2):865-878
- [165] Lundgren MR, Sultan SE. Seedling expression of cross-generational plasticity depends on reproductive architecture. *American Journal of Botany*. 2005;**92**(2):377-381
- [166] Galloway LF, Etterson JR. Plasticity to canopy shade in a monocarpic herb: Within- and between-generation effects. *New Phytologist*. 2009;**182**(4):1003-1012
- [167] Sultan SE. Phenotypic plasticity for offspring traits in *Polygonum persicaria*. *Ecology*. 1996;**77**(6):1791-1807
- [168] Sultan SE. Phenotypic plasticity for fitness components in *Polygonum* species of contrasting ecological breadth. *Ecology*. 2001;**82**(2):328-343
- [169] Sultan SE, Barton K, Wilczek AM. Contrasting patterns of transgenerational plasticity in ecologically distinct congeners. *Ecology*. 2009;**90**(7):1831-1839
- [170] Franks SJ, Sim S, Weis AE. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences of the United States of America*. 2007;**104**(4):1278-1282
- [171] Boyko A, Blevins T, Yao YL, Golubov A, Bilichak A, Ilnytskyy Y, et al. Transgenerational adaptation of *Arabidopsis* to stress requires DNA methylation and the function of Dicer-Like proteins. *PloS One*. 2010;**5**(3):e9514
- [172] Kou HP, Li Y, Song XX, Ou XF, Xing SC, Ma J, et al. Heritable alteration in DNA methylation induced by nitrogen-deficiency stress accompanies enhanced tolerance by progenies to the stress in rice (*Oryza sativa* L.). *Journal of Plant Physiology*. 2011;**168**(14):1685-1693
- [173] Steets JA, Ashman TL. Maternal effects of herbivory in *Impatiens Capensis*. *International Journal of Plant Sciences*. 2010;**171**(5):509-518
- [174] Donohue K, Schmitt J. Maternal environmental effects in plants: Adaptive plasticity? In: Mousseau T, Fox CW, editors. *Maternal effects as adaptations*. New York: Oxford University Press; 1998
- [175] Fitter AH, Fitter RSR. Rapid changes in flowering time in British plants. *Science*. 2002;**296**(5573):1689-1691
- [176] Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*. 2003;**421**(6918):37-42

- [177] Miller-Rushing AJ, Primack RB. Global warming and flowering times in Thoreau's concord: A community perspective. *Ecology*. 2008;**89**(2):332-341
- [178] Verhage L, Angenent GC, Immink RG. Research on floral timing by ambient temperature comes into blossom. *Trends in Plant Science*. 2014;**19**(9):583-591
- [179] Rosas U, Mei Y, Xie Q, Banta JA, Zhou RW, Seufferheld G, et al. Variation in *Arabidopsis* flowering time associated with *cis*-regulatory variation in *CONSTANS*. *Nature Communications*. 2014;**5**:3651
- [180] Banta JA, Ehrenreich IM, Gerard S, Chou L, Wilczek A, Schmitt J, et al. Climate envelope modelling reveals intraspecific relationships among flowering phenology, niche breadth and potential range size in *Arabidopsis thaliana*. *Ecology Letters*. 2012;**15**(8):769-777