THE ROLE OF AGE-STRUCTURE IN THE OPTIMAL GERMINATION FRACTION OF SEEDS

Amy K Webster[1], Rene M Cieszewski[†], Daniel EL Promislow[1,2]

[1]*Department of Genetics, University of Georgia, Athens, GA.*

[2]*Corresponding author, Department of Pathology and Department of Biology, University of Washington, Seattle, WA.*

ABSTRACT. In this review, we analyze Cohen's classic 1966 paper, "Optimizing reproduction in a randomly varying environment," and focus on how subsequent studies have relaxed Cohen's assumptions regarding age-structure. We do this in two ways, by analyzing studies that relax assumptions of age-structure in either the aging seed or the aging adult plant. Several studies have analyzed annual plants, which can exhibit age-structure due to seeds remaining dormant in the seed bank for one or more years. However, few studies have analyzed perennials with seed dormancy. These plants could have age-structure due to both dormant seeds and the aging plant, and thus could have much more complicated dynamics. Accordingly, here we share ideas and encourage future research in both the theoretical and experimental aspects of this field.

Keywords: Dormancy; age-structure; senescence; seed banks; annual; perennial; mathematical model.

1 INTRODUCTION

In 2005, scientists managed to germinate a date palm tree seed that had been dormant for 2,000 years (Sallon et al., 2008). This is an extreme example of the ability of some seeds to remain dormant in a seed bank over multiple seasons before successfully germinating (Evans and Dennehy, 2005). In contrast, the viviparous mangrove tree has seeds that germinate before they have even detached from the parent. Given that seeds must germinate before reproducing, how can we explain this extraordinary variation in seed dormancy, and why would selection favor seeds that do not germinate as soon as possible?

In this review, we discuss the evolutionary theory that has been developed to explain the existence of seed banks, which arise when seeds delay germination, remaining dormant for one or more years. With few exceptions, this theory has focused on delayed germination in seeds of annual plants. Annual populations, which live for one year, flower, and then die, lack age-structure. We can think of the seed bank as creating a kind of genetic age-structure, whereby the seeds of adults growing in a single, same-aged cohort germinate at different times. As we will discuss below, theoreticians have developed models to explain why seed germination can be

adaptive for annual species. But as our initial example illustrates, age-structured species can also produce seeds with delayed germination. Accordingly, we consider the importance of age-structure, both within the seed bank, where there can be seeds of different ages, and among adults for plants with perennial life cycles in which individuals survive over multiple seasons. Both factors have the potential to influence the selective forces acting on the evolution of delayed germination, and the seed bank in turn, could affect selection on perennial survival rates. In this brief review on age-structure and the seed bank, we discuss existing models and suggest areas where we think there are excellent opportunities for further research.

[†]b. 1991, d. 2011. Rene M Cieszewski worked as an undergraduate researcher at the University of Georgia under the supervision of Drs. Daniel Promislow and Jacob Moorad. Rene was interested in applying mathematical models to the problem of germination in age-structured populations. The title of his project was "Delayed Reproduction and Age/Class Structure in a Randomly Varying Environment". Unfortunately, Rene did not have the opportunity to complete this work. This paper, which was inspired by Rene's work and includes many of his ideas, is written in his memory.

2 Trade-Offs and Bet Hedging

In 1979, Law (1979) introduced the notion of a 'Darwinian Demon', an organism that faces no constraints of any sort, able to reproduce an infinite number of offspring and live forever. Of course, all organisms face constraints, and these constraints can lead to trade-offs. For example, we commonly see trade-offs between survival and reproduction. Individuals or species that have relatively high levels of reproduction early in life tend to be relatively short-lived. In fact, the organic world is filled with a diversity of different life-history strategies along a slow-fast continuum (Promislow and Harvey, 1990).

Traits such as growth rate, age and size at reproduction, size and number of offspring, and lifespan make up a plant's life history (Evans and Dennehy, 2005). In addition to these, plants can also vary in the number of seeds that germinate immediately versus those that remain dormant. Each of these traits can contribute to individual fitness. However, we typically find that these various traits trade off with one another, and the existence of the aforementioned 'Darwinian Demon' is impossible. The constraints that shape fitness trade-offs have led biologists to ask what the optimal strategy is for a given population. This optimal life history strategy is determined not only by the *mean* value of important abiotic factors (i.e., temperature, rainfall, soil chemistry, etc.) but also by the *variation* in the environment.

Consider the problem faced by an annual plant living in an environment that fluctuates from year to year. Once an individual has reproduced, it dies. However, it may have no way of predicting what the environment will be like when its offspring germinate. This leads to the following trade-off: In a growing population, there is a strong advantage associated with early reproduction. In this case, all of the seeds that a plant produces should germinate. But what if some years are so poor that few or no individuals that are recruited from the seed bank survive to reproduce? In this case, plants should be selected to spread reproduction out over several years so that at least some offspring are likely to survive.

By spreading out reproduction over multiple years, the plant avoids the reproductive extremes associated with either all seeds germinating or all seeds dying depending on the environmental conditions of a given year. While seeds that do not germinate the first year risk death in the seed bank, seeds that do germinate risk experiencing a poor year. This phenomenon of spreading out reproduction, known as bet-hedging, is accomplished by an annual plant by ensuring that some of its seeds enter a seed bank. In doing so, a certain fraction of the seeds produced do not immediately germinate but can stay dormant for one or more years. Due to the risk of dormant seed mortality, the mean annual fitness is decreased. However, since at least some of a plant's seeds are likely to germinate, annual variation in fitness is also decreased. By decreasing variation in fitness, an individual can increase its long-term geometric growth, which is advantageous for survival from an evolutionary perspective (Cohen 1966). Thus, a new seed has three possible options: germinate, enter the seed bank, or die (see Figure 1). The option of storing seeds can be adaptive for the plant if it allows its progeny to survive a fluctuating environment in which "bad" years occur, where germinated seeds die. Plants are effectively hedging their bets against a bad year. Thus arises a key question—how much to hedge?

3 A Mathematical Model of Bet-Hedging

In the 1960's, Dan Cohen was a Ph.D. student working on desert annuals. These plants face particular environmental challenges. Seeds need a rainfall event to germinate, grow, mature, and reproduce. However, a single rainfall, let alone two or more, is a rare commodity. In a bad year, every seed that germinates might die before it reproduces. If no seeds germinate, a good year might be missed, and the dormant seeds could experience the costs associated with an increased risk of decay. Thus, Cohen realized that there was likely to be an optimal germination fraction for the plant, and that it would depend on the variability of the environment and the underlying life history traits of the plant population. Cohen developed his now classic mathematical model to determine the optimal germination fraction of an annual plant in a variable environment that would maximize the long-term geometric mean growth rate of the population (Cohen, 1966).

Cohen's model relies on five key simplifying assumptions. First, he assumes that there is a risk associated with survival and reproduction in a varying environment such that there is a probability $0 = P = 1$ that a certain favorable environment Y will occur; second, seed germination is not density-dependent; third, a certain fraction of the seeds $0 = D = 1$ decay each year; fourth, a certain fraction $0 = G = 1$ will germinate each year; and fifth, the fraction that germinates remains constant from year to year. These assumptions can be seen explicitly through examination of the key elements of Cohen's equations, shown in Table 1.

Cohen's model demonstrates that the optimal germination fraction that produces the maximum long-term growth rate is affected by the proportion of good and bad years, the rate of decay, and the number of seeds produced per germinating seed (Figure 2). Cohen showed that the proportion of good and bad years had a much
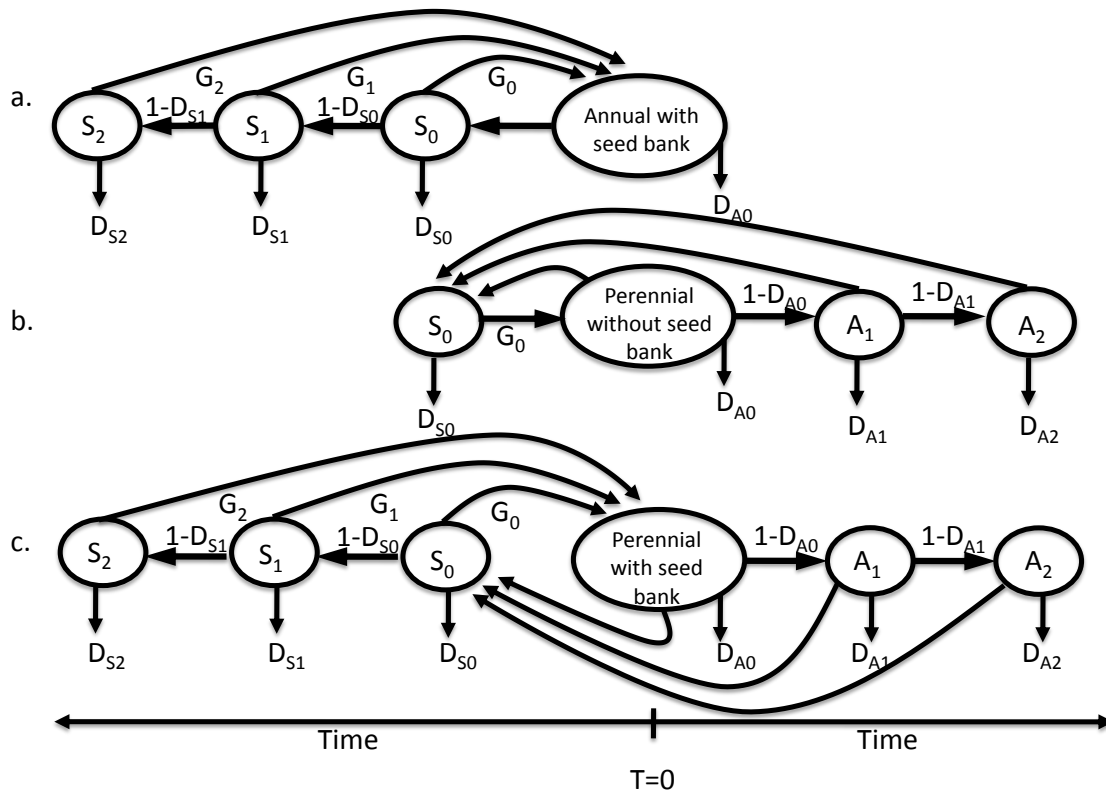
Figure 1: **Schematic illustrating types of age-structure in annuals, perennials without a seed bank, and perennials with a seed bank.** S_0 indicates the seeds produced by the parent plant, and each year spent in the seed bank is indicated by the addition of 1 in the subscript (S_1, S_2, etc.). A_0 represent an initial cohort of adult plants able to reproduce in their first year, and each subsequent year that the plant is able to reproduce is indicated by the addition of 1 in the subscript (A_1, A_2, etc.). G represents the fraction of seeds germinating from a given cohort of seeds. Of the seeds remaining after germination, a proportion D_S die, while $1-D_S$ remain in the seed bank. D_A represents the proportion of adults that die in a given year, while $1-D_A$ move on to live an additional year. Annuals exhibit age-structure through the persistence of the seed bank (a), while perennials without seed banks exhibit it through the persistence of the adult plant (b). Perennials with seed banks exhibit both types of age-structure, giving them more complicated dynamics (c).

stronger effect on the optimal germination fraction than the death rate such that G P, demonstrating the importance of environmental conditions on the strategy a plant adopts. Cohen's model was followed by numerous models that relaxed various of his simplifying assumptions (e.g., Kalisz and Mcpeek, 1992; Philippi, 1993; Rees, 1994; Dyer, Fenech, and Rice, 2000). Such studies have continued to increase in frequency since the publication of Cohen's paper in 1966 (Figure 3).

4 AGE STRUCTURE

Cohen's model focused on annual plants, as have most subsequent studies (reviewed in Hopper 1999, Evans and Dennehy 2005, Simons 2011). Surprisingly, few stud-

ies have looked at the effect of the age of seeds and of adults (the latter is relevant for perennials plants), especially in polycarpic species (ones that flower repeatedly). Why should we be interested in age-structure? In a series of classic papers published between the 1940s and 1960s, Peter Medawar, George Williams and W.D. Hamilton provided evolutionary explanations for the origin of senescence (Medawar, 1946; Medawar, 1952; Williams, 1957; Hamilton, 1966). Medawar's key insight was that the intensity of selection declines with age. Consider a novel deleterious mutation that decreases survival at just one age. If the effects of the mutation occur early in life, selection will most efficiently act to eliminate the mutation from the population. If, however, the effects are confined to very late age, then

Table 1: Equations used to develop Cohen's model

---

(1) $S_{t+1} = S_t - S_t \cdot G - D \cdot (S_t - S_t \cdot G) + G \cdot Y_t \cdot S_t$

    S_t : Number of seeds, S, at time t

    G : Fraction of seeds that germinates each year

    D : Fraction of seeds that decays each year

    Y: Fraction of seeds yielded for each germinating seed; varies based on environmental conditions

(2) $S_N = S_0 \cdot \prod_i [(1 - G) \cdot (1 - D) + G \cdot Y_i]^{n_i}$

    N : Number of years

    n_i : Number of times Y_i occurs in the sequence

(3) $\lim_{N \to \infty} \frac{\log S_N}{N} = \sum_i P_i \log[(1 - G) \cdot (1 - D) + G \cdot Y_i]^{n_i}$

    P_i : Probability of Y_i

(4) $G_{\max} = P_y - (1 - P_y) \frac{1-D}{Y+D-1}$

The number of seeds remaining in the seed bank from one year to the next is shown in **(1)**, and the number of seeds after N years is shown in **(2)**. After taking the logarithm of both sides and dividing by N, the equation can be simplified to **(3)**. Different values for P, G, D, and Y are tested in order to determine which value of G maximizes the long-term growth rate, which is the left side of equation **(3)**. Equation **(4)** gives an expression for the maximum value of G for the case when Y_i can assume the values of 0 or Y. This equation shows that for all but very small rates of decay, $G \approx P$.
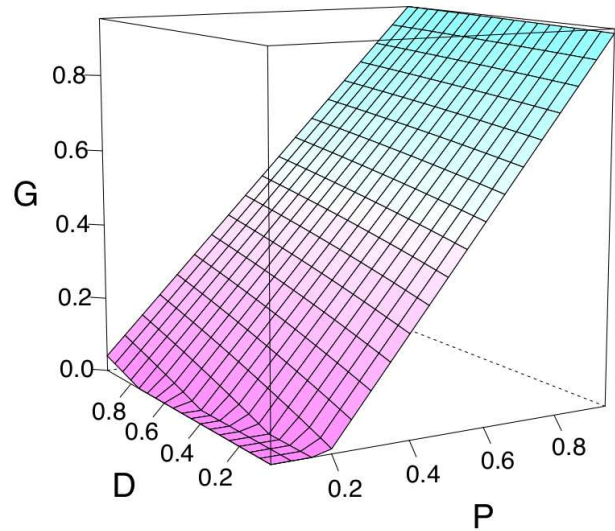

Figure 2: **Representation of germination fraction (G) in two environments with varying values of P and D that maximizes long-term growth rate.** Using equation (4) from Table 1, this graph shows the germination fraction, G, as a function of P and D assuming $Y=5$. P represents the probability that a given type of environment, Y, occurs. The graph models a situation in which there are two environments, with Y is equal to either 0 or 5. D represents the death rate of the seeds. The figure shows that P has a much stronger effect on the growth rate than D, meaning that P is a stronger predictor of the optimal germination fraction in an annual plant population.

these effects might not occur until well after all or most reproduction has taken place, and selection might allow the mutation to be passed on to the next generation. Over evolutionary time, Medawar argued, such late-acting mutations will accumulate and lead to senescence.

This principle applies to seed banks due to the fact that selection acting on the parent may shape germination strategies. The strength of selection declines with age, as does the residual reproductive value (Fisher, 1930). These factors might then give rise to optimal germination strategies that change with parental age. Thus, these factors are applicable for perennial trees with seeds that can survive multiple years (Dalling, Swaine and Garwood. 1998; Schmidt, Leuschner, Molder and Schmidt. 2009). Similarly, it is possible that the age of the seeds in the seed bank can affect the optimal germination fraction. Interestingly, since the decline in the force of selection begins with the onset of reproduction

(Hamilton 1966), at least in a constant environment the strength of selection on seeds should not decline as they age in the seed bank. Here we will review the existing experimental and theoretical studies that have relaxed Cohen's key assumption of no age-structure in seeds or plants by addressing the potential effects of seed and plant age. We will suggest specific areas that are ripe for future study concerning the role of age-structure in plants.

By age-structure, here we mean specifically the situation where reproduction can occur among overlapping generations (i.e., parents and their offspring). In plants, this overlapping age-structure can be present through delayed germination or through aging of the adult plant (Templeton and Levin, 1979; Tuljapurkar and Wiener, 2000). Annuals live only one year, reproduce, and die, so age-structure in annual plants can only occur through aging of the seeds in the seed bank. In this case, seeds of different ages coexist in the seed bank, while all of
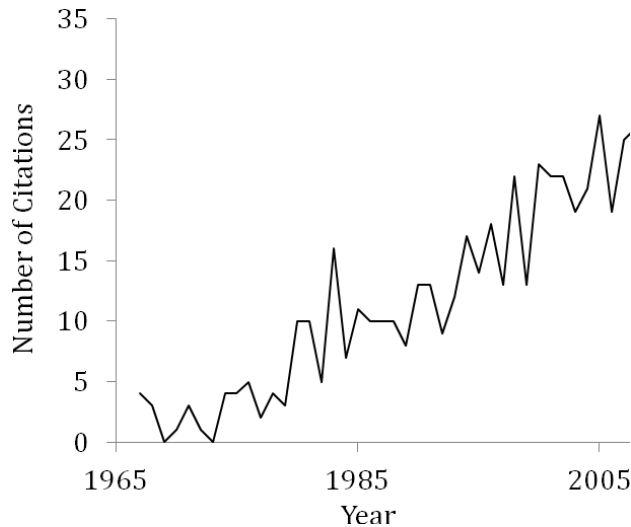
Figure 3: **Number of Citations Per Year for Cohen's 1966 Paper.**   According to data from Web of Science search engine, Cohen's paper has been cited in the literature concerning seed bank dynamics hundreds of times since its publication in 1966. The y-axis indicates the number of newly published studies citing Cohen's work in a given year. As this figure shows, the citation frequency has increased over time, showing its importance and relevance to current research.

the adult plants are the same age. Perennials with seed banks, in contrast, can experience both types of age-structure, with seeds surviving multiple seasons, or with plants of different ages reproducing at the same time. In this case, age-structure can cause the number of seeds produced and optimal germination fraction to vary depending on the age of the adult plant or the age of the dormant seeds. Perennials with seed banks, then, may have more complicated dynamics than annuals.

Studies that expand Cohen's model most frequently consider annual plants or perennials with minimal seed dormancy. Where perennials are considered, this is typically monocarpic perennials, which can live for many years, but then breed once and die. The seed bank dynamics of long-lived polycarpic perennials, such as trees, are largely unexplored. Both theoretical and experimental techniques have been used to aid in the analysis of this topic.

We note here that it is important to distinguish between monocarpic and polycarpic perennials. There can be age-structure in a monocarpic population, with individuals of different ages reproducing. However, aging theory (Hamilton 1966) suggests that selection intensity in monocarpic perennials will remain high and constant until the age at reproduction and death. In polycarpic perennials, by contrast, standard aging theory suggests

that selection intensity will decline with age. As we discuss towards the end of this review, how this decline in selection intensity is affected by seed banks remains an open question.

5   SEED AGE AND DENSITY DEPENDENCE

Seeds can germinate immediately, enter the seed bank, or die (Kalisz and McPeek, 1992). Because seeds produced in different years can coexist in the seed bank, there are different cohorts present. Seeds from different age classes can germinate in the same year, but the germination fraction for a given class could differ depending upon the age of the seed. Valleriani and Tielborger modeled this by assuming that seeds have age-specific germination fractions (Valleriani and Tielborger, 2006). This contrasts with Cohen's model, which assumes age-independent germination rates. In addition, this study also considers populations with and without density-dependence, as first developed by Ellner (1985). This takes into account the possibility that the presence of other plants alters the optimal germination fraction of seeds. In Valleriani and Tielborger's density-independent model, the resulting germination fraction turns out not to depend on seed age. However, in their density-dependent model, the germination fraction increases with the age of the viable seed. This is consistent with the authors' expectations—seed banks with few seeds are more likely to be composed of the oldest seeds, since others of the same class will already have germinated. In the case of density-dependence, only a finite number of plants can grow in a given area, so fewer seeds present in the seed bank correspond to a higher germination fraction. Thus, the older seeds in this model experience a higher germination fraction. In contrast, seed banks with many seeds will tend to be composed of mostly younger seeds and are more likely to experience a lower germination fraction. Experimental studies confirm the importance of density-dependence, but in contrast to the results of Valleriani and Tielborger, find that the germination fraction decreases with age under competitive conditions (Kalisz, 1991; Dyer, French and Rice, 2000).

Dormant seeds generally experience higher density upon emergence than those that germinate immediately, so effects of density on optimal germination fraction are important to consider (Dyer, French and Rice, 2000; Rice and Dyer, 2001). One such effect could include increased competition, since other existing plant species or plants of the same species have had additional time to grow and occupy space while some seeds remain dormant. In their study on the effect of seed age in two populations experiencing varying amounts of density, Rice and Dyer (2001) confirmed the importance of density-

dependence. While one population had equal fitness between new and old seeds, a second population had a lower germination fraction and slower germination among older seeds (Rice and Dyer, 2001). This second population experienced a denser environment than the first, and this shows that the effect of aging could be evident when the seeds experience competition upon emergence. Density-dependence was also a factor in another experimental study that examined the role of the seed bank in a natural population. Kalisz and McPeek (1991) studied seed age in the winter annual *Collinsia verna.* They found that an average of 36% of seeds emerged within the first year, 6% after two years, and 3% after three years. This decrease in germination fraction with seed age is consistent with Rice and Dyer and with the concept of seed decay but differs from the model proposed by Valleriani and Tielborger.

Researchers have also studied the effects of environmental variability on seed bank dynamics and population health. A theoretical study done by Kalisz (1992) analyzed growth rates of annuals with and without seed banks in varying environments. By using the growth rate data for "good" and "bad" years from a previous study (Kalisz, 1991), conditions for an annual with and without a seed bank were modeled to show the effects of the seed bank on the population's growth rate. While plants both with and without a seed bank had the same growth rate during good years, plants without a seed bank had a lower growth rate than plants with a seed bank during bad years. A separate experiment tested seeds under conditions of a good year followed by a good year (Philippi, 1993). When seeds experienced the same good conditions for two consecutive years, it was shown that seeds that do not germinate under a given set of conditions the first year occasionally germinate during the second year. In other words, individual seeds are not programmed to germinate in response to a certain set of environmental conditions. Rather, a certain fraction of the total number of dormant seeds germinates in a given year.

6   Age Structure in Perennials

Age structure in perennials contrasts with age-structure in annuals because it involves the aging of the adult plant in addition to its seeds. The question then arises: how does age-structure in perennials affect the growth rate of a population in contrast to age-structure in annuals? Templeton and Levin (1979) were the first to consider the effect of age-structure on the seed bank in plants. They used theoretical models to study the dynamics of seed banks in annuals, but also claimed that the dynamics influencing the growth rate of perennial plants past their juvenile stages are the same as annual

plants with a seed bank. This statement has since been tested through theoretical and experimental approaches and some interesting results have been found. Before turning to these results, it is worth noting that Templeton and Levin's claim resembles Lamont Cole's famous result (Cole, 1954). Cole noted that in order for an annual plant to match the fitness of an *immortal* competitor, it simply needs to produce one more offspring than the immortal individual. Of course, reality must be more complicated (Schaffer 1973), or we would live in a world consisting entirely of semelparous species.

In order to investigate the role of age-structure in plants with different growth strategies, Tuljapurkar and Wiener (2000) developed a model to test the idea that developmental delay and reproductive delay are the same with respect to a population's growth rate. Developmental delay can be understood through the context of an annual plant with a seed bank, since the dormant seeds delay their development by not germinating, despite good conditions. Reproductive delay, in contrast, involves a certain fraction of plants in a population delaying some or all reproductive effort to a later season, so that some of the plants are dormant for certain seasons. A plant undergoing seed dormancy saves some of its seeds for a year that may be more favorable, allowing for the possibility that future conditions are improved. A plant undergoing reproductive delay, in contrast, samples genotypes from the past by using an older plant to produce seeds. Perennial plants can reproduce over multiple years, but because they utilize reproduction from older plants, the effect of reproductive delay may be the same. In their model, Tuljapurkar and Weiner assume that both types of delay carry equal costs. Because both types of delay wager on the favorability of either the past or future, time reversibility is a critical assumption. This means that the environmental conditions follow a pattern that is independent of time's direction and sampling genotypes from the past or future does not make a difference. If time is reversible, the two methods of bet-hedging can be seen as equivalent. Also, Tuljapurkar and Wiener show that if one type of delay is present in a population, it is more adaptive to increase that type of delay rather than develop the other. By this model, then, perenniality trades off against seed dormancy. Therefore, it is common to see species with just one type of delay, and it may not be important which type of delay is present, but rather which type developed first.

Annual plants live for only a single reproductive season, so they cannot have the reproductive delay present in perennials. While Tuljapurkar and Wiener state that it is more adaptive to continue the type of delay that develops first, the reality is that some perennials do have seed banks, and thus exhibit two types of delay. How-

ever, later theory suggests that environmental variability can favor a combination of polycarpic reproduction and a seed bank (Wilbur and Rudolf 2006). Wilbur and Rudolf (2006) draw the important distinction between monocarpic perennials (modeled by Tuljapurkar and Wiener) and their own model of polycarpic (or iteroparous) perennials. In the latter case, environmental variability can favor both developmental delay and reproductive delay of polycarpic species.

Well before Tuljapurkar and Wiener's theoretical work, empirical studies examined whether one type of delay predominates in nature. For example, a study by Sarukhan (1974) looked at three species of perennial plants. One species reproduced mostly through seed production, one reproduced mostly vegetatively, and one used both types of reproduction. In both of the seed-producing species, the seeds were dormant for only a short time and a high proportion germinated, consistent with the Tuljapurkar and Wiener's (2000) prediction that one type of delay should predominate. Because these plants are perennials and can reproduce in subsequent years, it seems favorable for the seeds to germinate quickly. We see this pattern arise again in a study by Dyer et al. (2000) of a perennial grass that has low seed dormancy. Although perennials often do have seed banks (Dalling, Swaine and Garwood 1998; Schmidt, Leuschner, Molder and Schmidt 2009), in this case, the perennial grass best adapts by undergoing rapid germination instead of utilizing a seed bank.

While a perennial habit seems to sometimes favor increased germination rates, this same phenomenon can be seen in response to increased competition (Dyer, French and Rice, 2000). As with the seeds of an annual plant, there is more competition for germinating perennial seeds when other plants are present. However, because the parental generation of perennial plants need not die after producing seeds, these seeds have the potential for intergenerational intraspecific competition. Rice and Dyer (2001) showed that older seeds in annuals have a lower germination rate under dense conditions If the same applies to perennials, we would expect perenniality to favor rapid germination of seeds, due to this density-dependence effect (Rice and Dyer, 2001). This idea was explored by Tielborger and Prasse (2009), who tested for density-dependence of germination rate in four desert perennial plant species. Consistent with other studies, they found that both interspecific and intraspecific neighbors increased the rate of emergence of seeds. However, they found that in fact, merely the presence of neighbors increased germination rate. The number of neighbors was not important, meaning that at least in some species, seeds may sense the presence but not the quantity of their neighbors. We note that this study did not test for later emergence of seeds that did not germinate immediately, focusing simply on the current conditions that prevent or promote the germination of seeds from perennials.

In summary, theoretical and experimental studies of perennial plants have shown that the evolution of seed dormancy and longevity of the adult plant are both adaptations to variable environments. Among monocarpic perennials, theory suggests that if either developmental or reproductive delay exists, then this type should persist rather than another type of reproductive delay evolving (Tuljapurkar and Wiener, 2000). This has been confirmed experimentally by a study of perennial plants whose seeds have a rapid rate of emergence instead of remaining in a seed bank. Howver, while this method of rapid germination for seeds of perennial plants seems to be the most prevalent, but there do exist instances in which perennials exhibit seed dormancy (Vasquex-Yanes and Orozco-Segovia, 1993; Hanley, Unna, and Darvill, 2003; Walters, Midgley, and Somers, 2004; Ne'eman, Ne'eman, Keith, and Whelan, 2009), consistent with subsequent theory of polycarpic perennials (Wilbur and Rudolf 2006). While annuals can only introduce age-structure by germinating seeds of different ages, perennials introduce age-structure through production of seeds from adult plants of different ages and also, in some cases, through seed dormancy. We might expect that where the adult plant can delay reproduction, there is less of a need to delay germination. Theory suggests otherwise, but we are far from a comprehensive understanding of how selection shapes patterns of reproductive delay.

7 Future Directions

Most of the studies already done to expand Cohen's work concern the dynamics of annual plants. Models of monocarpic perennial species have shown how the dynamics of the reproductive delay of perennials are symmetric to those of the developmental delay of annuals under conditions of time reversibility and equal costs (Templeton and Levin, 1979; Tuljapurkar and Wiener, 2000; reviewed in Childs, Metcalfe and Rees 2010). Other experimental studies have shown that the presence of interspecific and intraspecific neighbors induces rapid germination, so utilizing a seed bank is not necessarily the optimal bet-hedging strategy in many species of perennials (Sarukhan, 1974; Dyer, French and Rice, 2000; Rice and Dyer, 2001; Tielborger and Prasse, 2009). It has been found that older annual seeds have a lower germination fraction in more dense environments. When seeds of perennials experience a rapid rate of emergence, this could be an adaptation to avoid the age-related costs associated with germination of older seeds in a dense environment. Taken together, the findings that we de-

scribe above point to at least four areas that are ripe for future research.

First, because seeds of annual plants experience reduced fitness with age, future studies should test whether seeds from perennials experience the same decline with age while germinating in competitive environments. Most previous studies have focused on the patterns of density-dependence, rather than the effect of seed age. Perennials also have the added dimension of age-structure due to parent plant age. We might observe an effect of adult senescence on seed quality, whereby older individuals produce poorer-quality seeds that have a germination probability influenced by the parent's age, rather than by the seed's age. It is likely that the seeds of perennials with seed banks would have an age-related decline in fitness similar to the seeds of annuals with seed banks. However, perennial seeds germinate immediately are likely to decay more rapidly because there is little selection favoring longevity in these seeds.

Second, according the models discussed above, for a monocarpic perennial the dynamics of reproductive delay and developmental delay are the same given that they have equal costs and exist in time-reversible environments. The cost of developmental delay is that a fraction of individuals that undergo delay will decay prior to germination, while the cost of reproductive delay is that some adults will not survive to reproduce. The assumption that these costs to delay are equal is another area that should be investigated through further research. We anticipate that the costs associated with the aging seeds of a seed bank are likely to be quite different from the costs associated with the germination of seeds produced by an aging plant. Additionally, the cost of having two types of delay, such as in the case of a perennial with a seed bank, could be different than having only one. Empirical studies should determine the costs associated with developing and maintaining both types of delay. In order to test the cost of reproductive delay, for example, measurements of the germination fraction of seeds produced by a perennial plant first reproducing at year x could be compared with previous measurements of the proportion of seeds from annuals exiting the seed bank from each age class. The age of the perennial plant could affect the number of seeds produced in addition to the viability of those seeds, so both should be tested. A recent study by Tuomi *et al.* (2013) investigates the idea of having both developmental and reproductive delay within a perennial plant, but models the dormancy by assuming the plant itself goes underground for one or more seasons, rather than producing seeds that do so. The model that matches the closest with the data is one that assumes that dormancy "resets" the plant's age to be independent of its predormant age. Future studies should consider the degree to which

plant dormancy and seed dormancy share similar evolutionary causal associations with life history strategies.

Third, recall that bet-hedging involves reducing the variance between years as a strategy for increasing long-term geometric mean fitness. In this light, for polycarpic perennials, we need to study the productivity in terms of the number of seeds produced each year and the viability of those seeds. Those values should be compared over multiple, environmentally variable years with the productivity of closely related annuals to assess further the effects of age-structure in perennials. This could be modeled by assuming that a perennial plant in a variable environment can produce a certain number of seeds in its lifetime, but that the adult plant experiences age-related costs. Without age-structure or constraints, the dynamics should be identical because an optimal fraction of seeds would "emerge" from the adult perennial plant rather than the seed bank each year. The effects of annual variability in risk of adult mortality, of senescence, and of trade-offs between investment among years all might affect the optimum strategy in ways that deviate from that of an annual plant and its seed bank.

Fourth, and perhaps most importantly, the conditions that cause seed dormancy in perennials need to be studied further, and might offer new modeling opportunities. For example, some fire-adapted perennial species with smoke-induced germination maintain seed banks that do not germinate unless they receive the correct environmental stimuli (Hanley, Unna, and Darvill, 2003; Walters, Midgley, and Somers, 2004; Ne'eman, Ne'eman, Keith, and Whelan, 2009). In these species, in which fire could potentially destroy the parent plant (eliminating both the source of additional seeds and competition against those seeds), a seed bank is necessary for population persistence. In tropical rainforests, some seeds remain dormant due to the presence of a hard coat that must become permeable through interactions with microorganisms, animal guts, high heat, etc., in order for the seed to germinate (Vasquex-Yanes and Orozco-Segovia, 1993). In these cases, the decision of whether or not a seed should germinate is heavily influeneced by environmental conditions. Unlike annual plants, in which a proportion of seeds remain dormant even in a good year, these cases indicate that dormant seeds of a perennial plant will, in fact, germinate under the conditions it deems "good." While these examples certainly do not account for all instances of seed dormancy with perennials, they indicate that the driving forces for seed dormancy in perennials may vary significantly from those of annuals. The startling diversity of age-structure among plant species can be present through the age of the seed in the seed bank, the age of the plant, or a combination of the two. The particular strategy of a species can be best understood through the context of its environ-

ment, and both theoretical and experimental studies of bet-hedging in plants should take this into account.

We end with a cautionary note. Evolutionary theory tells us that senescence, the decline in age-specific rates of survival or reproduction with increased age, occurs because of the age-related decline in the intensity of natural selection (Medawar 1946, 1952). This notion—that the intensity of selection changes with age—is the basis on which we assume that adult age might be an important variable shaping optimal germination fraction in plants. However, it is also worth noting the theory might not apply to plants as it does in animals. For example, in plant species that can be stage- as well as age-structured, we are only beginning to understand how selection intensity varies in stage-structured, or stage-age-structured populations (Steiner, Tuljapurkar, Coulson and Horvitz 2012) compared with age-structured populations. In virtually all animal species, whether studied in the lab or the wild, we observe senescence (Promislow, 1991; Bronikowski et al., 2002; Partridge and Gems, 2002; Moorad, Promislow, Flesness, and Miller, 2012). Strikingly, the same is not true of plants. While some show clear signs of aging, others do not (Roach, 1993; Vaupel, Baudisch, Dolling, Roach, and Gampe, 2004). In fact, it might be the case that the very phenomenon that we are aiming to study—namely, the effect of adult age on seed germination rates—could influence the evolution of senescence. The age at which individuals reproduce can have a strong influence on selection for survival (Charlesworth, 2001). In the case of the seed bank, paradoxically, even dead individuals can increase their fitness. It remains to be seen whether the very existence of a seed bank could mitigate the effects of age on selection in plant populations. Too few studies have considered the role of plant age on seed bank dynamics, and it is important to do so in order to fully understand the seed bank.

Acknowledgements

References

Bronikowski, A. M., S. C. Alberts, J. Altmann, C. Packer, K.D. Carey, and M. Tatar. 2002. The aging baboon: Comparative demography in a non-human primate. Proceedings of the National Academy of Sciences of the United States of America. 99(14): 9591-9595.

Charlesworth, B. 2001. Patterns of age-specific means and genetic variances of mortality rates predicted by the mutation-accumulation theory of ageing. J Theor Biol. 210(1): 47-65.

Childs, D. Z., C. J. E. Metcalf, and M. Rees. 2010. Evolutionary bet-hedging in the real world: empirical evidence and challenges revealed by plants. Proceedings of the Royal Society B-Biological Sciences 277:3055-3064.

Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. J Theor Biol. 12(1): 119-129.

Cole, L. C. 1954. The population consequences of life history phenomena. Q Rev Biol. 29(2): 103-137.

Dalling, J. W., M. D. Swaine, and N. C. Garwood. 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. Ecology 79:564-578.

Dyer, A. R., A. Fenech, and K.J. Rice. 2000. Accelerated seedling emergence in interspecific competitive neighbourhoods. Ecology Letters. 3(6): 523-529.

Ellner, S. 1985. ESS germination strategies in randomly varying environments. 1. Logistic-type models. Theoretical Population Biology. 28(1): 50-79.

Evans, M. E., and J.J. Dennehy. 2005. Germ banking: bet-hedging and variable release from egg and seed dormancy. Q Rev Biol. 80(4): 431-451.

Fisher, R. A. 1930. The genetical theory of natural selection. Oxford University Press, Oxford, UK.

Hamilton, W. D. 1966. Moulding of senescence by natural selection. J Theor Biol. 12(1): 12.

Hanley, M. E., J. E. Unna., and B. Darvill. 2003. Seed size and germination response: a relationship for fire-following plant species exposed to thermal shock. Oecologia. 134(1): 18-22.

Hopper, K. R. 1999. Risk-spreading and bet-hedging in insect population biology. Annu Rev Entomol 44:535-560.

Kalisz, S. 1991. Experimental-determination of seed bank age structure in the winter annual Collinsia-Verna. Ecology. 72(2): 575-585.

Kalisz, S., and M.A. McPeek. 1992. Demography of an age-structured annual - resampled projection matrices, elasticity analyses, and seed bank effects. Ecology. 73(3): 1082-1093.

Law, R. 1979. Optimal life histories under age-specific predation. American Naturalist. 114(3): 399-417.

Medawar, P. B. 1946. Old age and natural death. Modern Quarterly.2: 30-49.

Medawar, P. B. 1952. An unsolved problem in biology. London: H.K. Lewis.

Moorad, J. A., D.E.L. Promislow, N. Flesness, and R.A. Miller. 2012. A comparative assessment of univariate longevity measures using zoological animal records. Aging Cell. 11(6): 940-948.

Ne'eman, G., R. Ne'eman, D.A. Keith, and R.J. Whelan. 2009. Does post-fire plant regeneration mode affect the germination response to fire-related cues?. Oecologia. 159(3): 483-492.

Partridge, L., and D. Gems. 2002. The evolution of longevity. Current Biology. 12(16): R544-R546.

Philippi, T. 1993. Bet-hedging germination of desert annuals - beyond the 1st year. American Naturalist. 142(3): 474-487.

Promislow, D. E. L. 1991. Senescence in natural-populations of mammals - a comparative-study. Evolution. 45(8): 1869-1887.

Promislow, D. E. L., and P.H. Harvey. 1990. Living fast and dying young - a comparative-analysis of life-history variation among mammals. Journal of Zoology. 220: 417-437.

Rees, M. 1994. Delayed germination of seeds - a look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. American Naturalist. 144(1): 43-64.

Rees, M., C. Jessica, E. Metcalf, and D.Z. Childs. 2010. Bet-hedging as an evolutionary game: the trade-off between egg size and number. Proc Biol Sci. 277(1685): 1149-1151.

Rice, K. J., and A.R. Dyer. 2001. Seed aging, delayed germination and reduced competitive ability in Bromus tectorum. Plant Ecology. 155(2): 237-243.

Roach, D. A. 1993. Evolutionary senescence in plants. Genetica. 91(1-3): 53-64.

Sallon, S., E. Solowey, Y. Cohen, R. Korchinsky, M. Egli, L. Woodhatch, and M. Kisley. 2008. Germination, genetics, and growth of an ancient date seed. Science. 320(5882): 1464-1464.

Sarukhan, J. 1974. Studies on plant demography: Ranunculus Repens L., R. Bulbosus L. and R. Acris L.: II. Reproductive strategies and seed population dynamics. Journal of Ecology. 62(1): 151-177.

Schaffer, E. L. C. W. M. 1973. Life history consequences of natural selection: Cole's result revisited. American Naturalist.107: 791-793.

Schmidt, I., C. Leuschner, A. Molder, and W. Schmidt. 2009. Structure and composition of the seed bank in monospecific and tree species-rich temperate broad-leaved forests. Forest Ecology and Management 257:695-702.

Simons, A. M. 2011. Modes of response to environmental change and the elusive empirical evidence for bet hedging. Proc Biol Sci 278:1601-1609.

Steiner, U. K., S. Tuljapurkar, T. Coulson, and C. Horvitz. 2012. Trading stages: Life expectancies in structured populations. Exp Gerontol 47:773-781.

Templeton, A. R., and D.A. Levin. 1979. Evolutionary consequences of seed pools. American Naturalist. 114(2): 232-249.

Tielborger, K. and R. Prasse. 2009. Do seeds sense each other? Testing for density-dependent germination in desert perennial plants. Oikos. 118: 792-800.

Tuljapurkar, S., and P. Wiener. 2000. Escape in time: stay young or age gracefully? Ecological Modelling. 133(1-2): 143-159.

Tuomi, J., E.E. Crone, J.R. Gremer, A. Jakaleniemi, P. Lesica, B. Pedersen, and S. Ramula. 2013. Prolonged dormancy interacts with senescence for two perennial herbs. Journal of Ecology. 101: 566-576

Valleriani, A., and K. Tielborger. 2006. Effect of age on germination of dormant seeds. Theoretical Population Biology. 70(1): 1-9.

Vasquez-Yanes, C. and A. Orozco-Segovia. 1993. Patterns of seed longevity and germination in the tropical rainforest. Annual Review of Ecology and Systematics. 24: 69-87.

Vaupel, J. W., A. Baudisch, M. Dolling, D.A. Roach, and J. Gampe. 2004. The case for negative senescence. Theoretical Population Biology. 65(4): 339-351.

Walters, M., J.J. Midgley, and M.J. Somers. 2004. Effects of fire and fire intensity on the germination and establishment of Acacia karroo, Acacia nilotica, Acacia luederitzii and Dichrostachys cinerea in the field. BMC Ecol. 4. 3.

Wilbur, H. M. and V. H. W. Rudolf. 2006. Life-history evolution in uncertain environments: Bet hedging in time. American Naturalist 168:398-411.

Williams, G. C. 1957. Pleiotropy, natural-selection, and the evolution of senescence. Evolution. 11(4): 398-411.