

SEED ECOLOGY, DORMANCY, AND GERMINATION: A MODERN SYNTHESIS FROM BASKIN AND BASKIN¹

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The names Baskin and Baskin will be as familiar to readers interested in the ecology of seed germination as “radicle” and “plumule.” It is Jerry Baskin who has the role of plumule in this scientific partnership, being the more visible (first named) author on the majority of the some 250 publications the Baskins have produced in the last three decades, but radicles become taproots and it is Carol Baskin who is senior author of this book with its massive accumulation of knowledge about seed germination that runs to more than 600 pages. It is interesting to learn that these partners were introduced to each other as well as to what has become the subject of their lifetimes’ work at the same moment in 1966 when chance determined they were to share a student project on the germination of *Sporobolus vaginiflorus* and *Aristida longespica*.

Seeds can exhibit notoriously idiosyncratic germination behavior, sometimes varying as much among the progeny of a single maternal parent as they do among different species. This has made for a voluminous literature composed mainly of minutiae and, at least until relatively recently, lacking in synthesis. When I first became interested in this subject myself in the mid-1970s its “bible” was in fact not a work of synthesis but *The Bibliography of Seeds* by Lela V. Barton, to whom (along with Marianna G. Nikolaeva) the book under review is dedicated. I well remember the feeling of excitement when I finally obtained my own copy of *The Bibliography of Seeds* in a used bookstore in New York for \$5. I only later discovered how difficult it was to extract any generalizations from the volume and why anyone had been prepared to part with it so cheaply. My copy has long sat on a top shelf, out of easy reach, in my office. Have Baskin and Baskin unscrambled the literature of seed germination sufficiently for their book to escape the same fate as Barton, quite apart from the fact that it is unwise to place any hardback book weighing 1.8 kilos on a top shelf? If it is to be successful, unscrambling requires at least three operations: first, methodological issues must be addressed, suspect findings must be eliminated and a core of reliable observations must be assembled; second a classification of seed dormancy traits needs to be devised and used to catalog the data; third, an ecological and evolutionary synthesis is needed.

METHODOLOGICAL ISSUES

The result of a germination test can be affected by how seeds are collected, by the conditions and period of stor-

age, and by when and how the test is performed. So, how can laboratory studies tell us anything about the ecology of germination in the field? This crucial issue is addressed right at the start in a chapter entitled “Ecologically meaningful germination studies.” Its message is that seeds must be collected, stored, and tested under conditions that are as near the natural as possible. Seeds should be collected only when ripe, tested immediately after harvest, or stored under actual or simulated field conditions, and natural dispersal units (such as grass caryopses) should be used without scarification or other treatment. Testing germination under naturalistic conditions means that seeds must be exposed to diurnally alternating temperatures equivalent to those occurring in the field and that this treatment should be crossed with two light treatments: the natural daily photoperiod and constant darkness to simulate burial. The dormancy status of many seeds changes seasonally, in some species even when they are in dry storage, so germination tests should be repeated at frequent intervals through the year and it is desirable to use several alternating temperature regimes on each occasion so that the changing response of seed germination to temperature can be tracked.

A consequence of long-term seed dormancy is that seeds accumulate in soil, sometimes reaching staggeringly high densities (up to 6×10^5 seeds/m² have been recorded). Baskin and Baskin have scrutinized the literature on seed banks and, with their characteristic concern for methodological detail, find that over half of density estimates include newly dispersed seeds, which may only be transients through the seed bank, so that the true size of the persistent seed bank is unknown in these cases. The miscreant studies are tabulated! The longevity of buried, dormant seeds is one of the wonders of botany with the record, accredited by radiocarbon dating of tissue from germinated seeds, reaching nearly 1300 years. Shorter, but still considerable, longevities in the soil of 50 or more years are quite commonplace for seeds of annual and biennial plants. Ongoing DNA repair is essential to retain viability for such long periods and, since it also appears that many of these seeds undergo annual dormancy cycles, it is clear that they are far from physiologically inactive during dormancy.

A CATALOG OF DORMANCY

By no means all published germination studies conform to the Baskins’ protocols, but even excluding the studies that do not leaves a substantial literature covering more than 3500 species. These species possess a bewildering variety of germination responses for which there is, as yet, no universally accepted classification. Part of the problem

¹ *Seeds: ecology, biogeography, and evolution of dormancy and germination*. C. C. Baskin and J. M. Baskin. Academic Press. 1998. 666 pp. \$99.95. ISBN 0-12-080260-0 (Hard cover).

lies in the fact that the underlying mechanisms that control dormancy are poorly understood. Baskin and Baskin subscribe to a classification of dormancy types, based upon the system of Nikolaeva (1977), which divides dormancy types into those that are "endogenous" and due to properties of the embryo and those that are "exogenous" and result from properties of the endosperm or any other tissues of the seed or fruit. What Harper (1959) and others term "enforced dormancy," where seeds are prevented from germinating by external constraints such as a lack of moisture, Baskin and Baskin describe as "non-dormancy." They are equally dismissive of Harper's term "induced dormancy" on the grounds that "we are unaware of a species whose seeds are nondormant at maturity that have been induced into dormancy," implying that "induced dormancy" is merely a kind of secondary dormancy. Harper's third dormancy type, "innate dormancy," covers all the multifarious kinds of endogenous and exogenous dormancy described in this book.

Three types of endogenous and three types of exogenous dormancy are distinguished. Endogenous dormancy may result from (1) a physiological inhibiting mechanism in the embryo ("physiological dormancy" or "PD"), (2) an undeveloped embryo (confusingly called "morphological" dormancy, or "MD"), or (3) from a combination of 1 + 2 called "morphophysiological" dormancy (MPD). The three primary types of exogenous dormancy are (1) "physical," caused by seed- or fruit-coat impermeability to water, (2) "chemical," due to germination inhibitors, and (3) "mechanical," caused by woody structures that restrict growth. Seeds with only a light requirement for germination are regarded as "non-dormant," even though such behavior in buried seeds must surely be logically classed as some form of functional dormancy.

Nikolaeva's scheme divides PD into three subcategories: "Nondeep PD," "Intermediate PD," and "Deep PD," according to the treatments required to break dormancy. In the first two of these, which include a large number of weeds and crops of commercial importance, embryos will actually grow and produce normal seedlings when excised from dormant seeds. This calls into question whether these forms of PD are genuinely endogenous (controlled by the embryo) as Nikolaeva's definition requires, and leads Baskin and Baskin to consider two possible explanations of the apparent contradiction. Either, there may be interactions between embryo and other tissues, or excision of the embryo may produce wound-induced ethylene that breaks dormancy. They conclude that "It seems reasonable that although embryos excised from seeds with nondeep PD grow normally, they are probably involved in controlling germination of intact seeds" because "dormancy-breaking treatments *per se* do not seem to have much effect on covering structures." Thus we have two pieces of negative evidence with apparently conflicting implications: embryos may not be responsible for PD because they germinate when separated from covering structures, and covering structures may not be involved because dormancy-breaking mechanisms don't affect them!

The Baskins argue that the answer is that PD is the product of an interaction between maternal seed coats and embryonic growth. Dormancy loss is accompanied by an increased "push power" from the embryo and germination

takes place when the embryo is finally strong enough to break through its maternal envelope. More positive evidence is clearly needed, and in the mean time I would be cautious about a classification of seed dormancy that is based (at least in the case of the two major types of PD) upon mechanisms that have yet to be satisfactorily elucidated. Baskin and Baskin come to a similar conclusion themselves in the case of one of Nikolaeva's exogenous mechanisms: "it is hard to be sure if there are any cases of true chemical dormancy because the effects of inhibitors in many studies have been tested on seeds after PD was broken."

Despite reserving judgement about certain subtypes of endogenous and exogenous dormancy, I believe that there are good evolutionary and genetic reasons to expect the dichotomy between embryo-controlled (endogenous) and maternally controlled (exogenous) mechanisms to be a fundamental one. In outcrossing populations the embryo shares only half its genes with its mother, while the polyploid endosperm is predominantly maternal (e.g., 2:1 in *Polygonum*-type development and 4:1 in *Lilium*-type development). There is thus the potential for genetic conflicts between mother and embryo and between embryo and endosperm over resource provisioning and the timing of germination (Westoby and Rice, 1982). For example, a maternal parent may raise her fitness by hedging her bets in a temporally varying environment, using dormancy to spread the germination of her offspring over two or more seasons. By contrast, individual seeds have only one shot at germination and, if dormancy were entirely embryo-controlled, should all germinate at one long-run optimum date. Such conflicts are invariably resolved in favor of maximizing the mother's fitness because she holds all the aces (Westoby, 1981); she controls seed provisioning, she can retard embryo development (or advance seed dispersal), and she envelops the embryo in layers of tissue that can control its access to water, light and oxygen. This is perhaps why the independent role of the embryo in physiological dormancy is so difficult to pin down. One way to quantify the contributions of maternal, paternal, and embryonic genes to dormancy is to conduct breeding experiments between inbred lines that differ in dormancy characteristics. The few studies of this type reported by Baskin and Baskin suggest, as one might expect, that maternal genotype is more important than paternal genotype (expressed through the embryo) though the latter does have significant effects in at least some cases. In fact, not only maternal genotype but also local maternal environment (including position on the plant) has a strong influence upon the dormancy of seeds.

The occurrence of physical dormancy is more easily demonstrated, since it results from the impermeability of maternal tissue (seed or fruit coats) to water and is also only rarely found in combination with PD. It is fascinating to learn that 12 of the 15 families known to contain species with physical dormancy possess large embryos and that these embryos, rather than the endosperm, store most of the food reserves of the seed. This pattern is consistent with the evolutionary hypothesis that, perhaps having lost the physiological control of germination that can be exercised through regulation of the food supply when this is held in the endosperm, maternal genes control it by physical means instead. This hypothesis should be susceptible to a phylo-

genetic test for whether the evolution of physical dormancy, and possibly of other exogenous dormancy mechanisms, correlates (perhaps with a delay) with an evolutionary shift in food stores from endosperm to embryo.

ECOLOGICAL AND EVOLUTIONARY SYNTHESIS

Even a half-awake reader of the foregoing paragraphs will have noticed the slide from a discussion of how dormancy is classified to a discussion of its evolution. Baskin and Baskin display no such indiscipline, reserving most of their discussion of the evolution of dormancy to the final chapter, which is entitled "Biogeographical and evolutionary aspects of seed dormancy." It is impossible not to look for evolutionary patterns in the wealth of comparative data that form the bulk of this book. For example, in Chapter 4 the authors discuss in great detail the dormancy cycles found in many short-lived plants. Dormancy cycles have been reported in annuals belonging to 40/44 genera (91%) investigated, but in polycarpic perennials in only 11/21 genera (52%). This is consistent with theory that predicts a negative correlation between the longevity of the mature plant and the longevity of its seeds in the soil, but the reader who does not know the relevant theoretical literature is not introduced to it until much later. Likewise, in Chapter 5, I couldn't resist wondering what adaptive function double dormancy might serve. Baskin and Baskin are quite right to complain, as they do later, that theoreticians should broaden their attention to the function of dormancy syndromes more complex than PD, and here is a prime candidate. Seeds with double dormancy require two cold seasons to fully germinate; the first cold stratification releases the radicle and the second releases the shoot, so that seeds require two years for germination. The syndrome is practically confined to the Liliaceae, and the delay in emergence above ground caused by double dormancy is reminiscent of the situation in another monocot family, the orchids, terrestrial species of which acquire a fungal symbiont before emerging above ground. Does mycorrhizal infection play a role in double dormancy in lilies?

Any reader of this book will find plenty of material in it for their own *à la carte* synthesis (and speculation), but what is offered by the table d'hôte in the concluding chapter? The findings in this chapter are based on a database of 3580 species whose germination ecology is described or tabulated in earlier chapters that deal with specific habitats or particular life histories. The first and major point that comes out of these data is that, with the exception of rain forest, the majority of species in all types of habitat display some form of seed dormancy, and that this is most often of the physiological type. Only in tropical deciduous forest is any other dormancy type, namely physical dormancy, nearly as common. Differences between habitats are most distinct in the tropics and subtropics ($n = 1452$ spp.) where there is an extremely clear trend from non-dormancy to dormancy (all types combined) across a habitat gradient from wet tropical rain forest (60% non-dormant) at one end through tropical deciduous forest (20% non-dormant) to hot deserts (<10% non-dormant). Though all these habitats are seasonal to some degree (because even rain forests have sea-

sonal rainfall patterns) environmental uncertainty increases with decreasing rainfall along the gradient. In temperate and arctic floras at least 60% of species ($n = 2128$ spp.) are dormant in all habitats, but there is no clear correlation with temperature or precipitation.

The second half of the final chapter is concerned with the phylogeny of seed dormancy, approached through the evidence of the fossil record and the distribution of dormancy types among extant angiosperms. Available fossil evidence suggests that early gymnosperms lacked seed dormancy, but is inconclusive in the case of early angiosperms. The phylogenetic scheme of Takhtajan (1980) is used to compare the distribution of dormancy types among angiosperm orders, and records of first appearance of families in the fossil record are used to date possible origins of dormancy types. The conclusions from this exercise are not very illuminating: most orders that contain families with non-dormant seeds also contain families with PD; the time of a family's appearance in the fossil record does not predict the type of dormancy found in its extant members; extant species belonging to families that first appeared as early as the Cretaceous display the full range of known types of dormancy, as well as non-dormancy.

More positively, based mainly upon physiological, embryological, and ecological grounds, Baskin and Baskin suggest a number of possible evolutionary transitions between dormancy types. For example, the presence of morphological dormancy in the Magnoliales may indicate a "primitive" condition from which non-dormancy could have evolved along with more fully developed embryos. Drier climates would favor the evolution of PD from non-dormancy, climatic cooling would favor deep PD, and so on. These kinds of ideas can nowadays be tested against an increasingly reliable angiosperm phylogeny, and it is a great opportunity missed that, with so much detailed information at their disposal, Baskin and Baskin did not try to do so using the molecular phylogeny of Chase et al. (1993), or a more recent equivalent. But, rather than criticize authors who have labored so hard already, let us thank them for a monumental work, which has successfully sifted and sorted the literature of germination ecology, leaving us with a firm foundation on which to build even greater synthesis. One thing is for sure: for some time to come this book will reside on my desk and not on a top shelf.

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