Seed Science Research (2017) **27**, 61–64 doi:10.1017/S0960258517000149

Seed ecology: a diverse and vibrant field of study

Carol C. Baskin*

Department of Biology, University of Kentucky, Lexington, KY 40506-0225 USA and Department of Plant and Soil Sciences, University of Kentucky, Lexington, KY 40546-0312, USA

Abstract

My purpose is to introduce a special issue of *Seed Science Research* devoted to papers resulting from material presented at Seed Ecology V held in Caeté, Brazil on 21–25 August 2016. An overview of the field of seed ecology is presented that includes a short summary of what I consider to be the eight basic subcategories of this field, and the five new areas of investigation that have developed as extensions and/or recombinations of basic areas. Seed ecology conferences allow researchers to communicate with each other and build new collaborative relationships. At Seed Ecology V, information was presented that related to each area of seed ecology. The nine papers in this special issue are a small sample of the information presented at the meeting, and each paper is briefly described and placed into one of the subcategories of seed ecology research.

Keywords: climate change, germination requirements of non-dormant seeds, intraspecific variation, phylogeny and seed traits, pollination and seed germination, seed dispersal, seed dormancy break

Introduction

This special issue of *Seed Science Research* is devoted to seed ecology, and the papers have their origin in material presented at Seed Ecology V held in Caeté, Brazil on 21–25 August 2016. It was an honour to work with the authors of these papers, and now as editor of this special issue I have the responsibility of writing the introduction for it. I personally strongly embrace the field of seed ecology, and part of the reason for my enthusiasm is that this field is highly diverse and has a large overall objective. As seed ecologists, what we would really like to know is: how do various biotic and abiotic factors influence every stage in the life of the seed, beginning with flowers and ending with a well-established, healthy seedling? This clearly is a complicated and multifaceted issue, but much progress now has been made on all of its fascinating parts. In fact, the body of knowledge gained from seed ecology research done thus far is so large that we need to subdivide the field. Thus, before we consider the new material presented in Brazil, I think a short review of what I consider to be the eight basic subcategories of seed ecology is in order.

Overview of the field of seed ecology

1. ***Pollination***

   At the level of the flower, the source of the pollen may affect germination percentages and rates of the resulting seeds. Thus, attention has been given to self- *vs* cross-pollination, and this has led to considerations of the size of plant populations, fragmented populations, near- *vs* far-neighbours and ultimately to inbreeding (and outbreeding) depression or the lack thereof on germination characteristics of the seeds. Furthermore, when introducing seeds from one population to another for restoration, consideration needs to be given to the possibility that outbreeding depression would occur in the subsequent generations.
2. ***Genetics* (*G*), *environment* (*E*) (*including epigenetic*) *and G × E effects on seeds***

   Seed dormancy and germination responses can be strongly influenced by genetics, and many studies have found genetic differences between populations. However, the environment of the mother plant before (sometimes) and after (mostly) zygote formation can have an effect on germination of the offspring, i.e. the seeds. Various factors of the mother plant environment such as temperature, photoperiod, amount and timing of precipitation, soil nutrient levels and competition from other plants may affect the dormancy and germination characteristics of the seeds. Furthermore, genetics of the parent plants can interact with environmental factors and influence the germination characteristics of seeds, and these transgenerational effects can carry over to the second generation and beyond.
3. ***Seed dispersal***

   The dispersal agents for seeds are wind, water, gravity and animals (including humans), and there could be both primary and secondary dispersal.

* Correspondence
Email: ccbask0@uky.edu

Seeds may be deposited on the soil surface, under litter, on tree bark, in mud in a body of water or deep in soil or sand, and the habitat to which they are dispersed may be fully exposed to the sun or to plant canopy shade with filtered light. Animal dispersal of seeds has received, and continues to receive, much research attention because, depending on the kind of seed, kind of animal and what the animal does to or with the seed, germination of seeds may be increased, decreased or not affected.

4. ***Seed dormancy***

   At the individual species level, one of the first objectives of many research projects is to determine via observations and experiments if seeds are dormant, and if so, what kind of dormancy do they have. Also, information as to whether seeds are desiccation sensitive or desiccation tolerant facilitates planning for seed storage and/or dormancy-breaking treatments. With the broad objective of planning experiments to determine how dormancy is broken in nature, it is important to know the kind of dormancy (or non-dormancy) and the environmental conditions seeds experience in the habitat between the time of seed dispersal and germination.

5. ***Dormancy-breaking requirements***

   Dormancy-breaking treatments required to promote germination vary with the kind of dormancy. For example, if seeds are water permeable and are dispersed in spring in the temperate zone they may require exposure to dry, warm (≥15°C) summer conditions for after-ripening (dormancy-break) to occur and germinate in autumn. On the other hand, some spring-produced seeds require warm (≥15°C, moist) and/or cold (*ca* 0 to 10°C, moist) conditions for dormancy to be broken, and germination occurs in autumn or spring, depending on the species. Most autumn-produced seeds in temperate zones require a cold moist treatment and germinate in spring, but some require warm and cold and thus cannot germinate until the second spring. In the case of seeds with water-impermeable seed or fruit coats (physical dormancy, PY), high temperatures of summer may make seeds sensitive to the low-temperature, dormancy-breaking (opening of water gap) conditions in autumn. However, low temperatures of winter may make seeds sensitive to the high-temperature, dormancy-breaking conditions in summer.

6. ***Germination requirements of non-dormant seeds***

   Non-dormant seeds of each species have a minimum, optimum and maximum temperature for germination, and light can promote, inhibit or have little or no effect on germination percentages and rates. Clearly, seeds need to be imbibed to germinate, but they vary in their tolerance of moisture stress and salinity stress. For some species, special environmental signals such as flooding, chemicals released from burning vegetation, exudates from roots of host plants (obligate parasites) or presence of a specific fungus (mycoheterotrophs) are required to promote germination.

7. ***Seed banks***

   All seed-producing plant species have non-germinated seeds that persist in the habitat until the first germination season, i.e. a transient seed bank. A persistent seed bank consists of non-germinated seeds that live in the habitat, often for many years, i.e. through multiple germination seasons, and seeds can be stored in the canopy of plants (aerial seed bank, i.e. serotiny) or in/on the soil. Although seed bank studies have been done in a wide range of habitats and in many parts of the world for a long period of time, this remains an active area of research. Currently, the effects of environmental factors such as fire, flooding, succession and invasive species on the composition of the soil seed bank are being investigated.

8. ***Ecological and fitness consequences of timing of seed germination***

   The timing of germination can have important consequences on whether or not seedlings live, and also on the life history characteristics of the plants that survive. For example, in temperate regions many seedlings from autumn-germinating seeds of annuals may die, but those that survive produce large plants with numerous fruits and seeds the following spring. On the other hand, if seeds of the same annual species delay germination until spring, survival percentages may be very high but the number of fruits and seeds produced per plant is low compared with that of plants from autumn-germinated seeds. Clearly, plants from seeds that germinate in autumn *vs* those that germinate in spring are subjected to very different environmental conditions, especially in the early stages of the life cycle, and increasingly researchers are asking: how does selection act on these two very different cohorts of plants? Also, timing of seed germination is of great concern to weed scientists, and, consequently, it is an important part of weed emergence models.

As research in the various areas of seed ecology (described above) has advanced, some new areas of investigation have developed. These exciting new areas, in many respects, are extensions and/or recombinations of the established areas.

Climate change. The impacts of global warming on seed production, characteristics of offspring (seeds), dormancy-breaking and germination requirements, formation of seed banks and life history traits are considered.

Habitat restoration. Information is needed on seed production and dispersal, presence (or absence) of dormancy, kind of dormancy, dormancy-breaking and germination requirements and formation of seed banks.

Evolution of dormancy. The determination of origins and evolutionary relationships of non-dormancy and the kinds of dormancy is based on phylogenetic relationships of plant families and on data for each family with regard to the presence of non-dormancy and of the kind(s) of dormancy.

Phylogenetic relationships of seed and life history traits. The phylogenetic relationships of plant taxa are increasingly being used to identify the relationships of taxa in terms of seed size/mass, germination and other life history traits.

Seed ecology at the molecular level. The great advances in molecular biology are making it possible for researchers to study the involvement of genes in the dormancy-breaking process in nature and the induction of dormancy at the end of the germination season, i.e. when conditions are no longer favourable for germination. This area of research benefits from knowledge of the kind of dormancy in seeds and of the environmental conditions in nature between the time of seed dispersal and germination. Thus far, this kind of research has concentrated on seeds with non-deep physiological dormancy (PD) that exhibit annual dormancy cycling in nature, but in the future studies need to be done on seeds with morphophysiological dormancy. Furthermore, I know of only one study that has tested for annual dormancy cycling in the PD component of combinational dormancy (PY + PD).

Seed ecology conferences promote communication

Many scientists throughout the world are devoted to studying one or more aspects of seed ecology; thus, it is natural that they want to communicate with each other. Although numerous papers on seed ecology are published in a wide array of journals each year, it is important for those in the field to have an opportunity to meet each other and to discuss their research. This need for personal communication by members of the seed ecology community has been met by the International Society for Seed Science, which to date has sponsored five International Seed Ecology Conferences: Seed Ecology I in Greece in 2004; Seed Ecology II in Australia in 2007; Seed Ecology III in the USA in 2010; Seed Ecology IV in China in 2013; and Seed Ecology V in Brazil in 2016.

The programme for Seed Ecology V included six keynote addresses, 44 oral presentations and 30 posters. Each presentation at Seed Ecology V can be, more or less, fitted into one of the subcategories of seed ecology: Climate change, Dormancy-breaking requirements, Ecological and fitness consequences of timing of seed germination, Evolution of dormancy, Genetics (G), environment (E) (including epigenetic) and G × E effects on seeds, Germination requirements of non-dormant seeds, Habitat restoration, Seed banks, Seed dormancy, Seed dispersal, Phylogenetic relationships of seed and life history traits, Pollination and Seed ecology at the molecular level. Thus, new information was presented at the 2016 meeting that made a contribution to each of the subcategories of seed ecology, as I have subdivided the field.

The papers in this special issue

The nine papers in this special issue of *Seed Science Research* are only a small sample of the information presented at Seed Ecology V, but they are a good sample of the diversity of the presentations. Each paper in the special issue has been fitted into a subdivision of seed ecology and will be described briefly.

Climate change. Anne Cochrane tested seeds of 26 *Eucalyptus* species from Western Australia for germination on a bi-directional temperature gradient plate and used the data to model seed germination responses to increased temperatures due to global warming. The model predicted that germination of some species will decline with increased habitat temperatures, but germination of many species will remain the same or be improved. However, large decreases in rainfall are generally predicted; thus, moisture stress may be highly detrimental to seedling survival.

Dormancy break. L. Felipe Daibes *et al*. investigated the effects of temperature on breaking physical dormancy (PY) in seeds of four legumes from the Cerrado (open savannas) in Brazil. Fire destroyed seeds on the soil surface, but heat from fires broke dormancy of seeds buried in soil. For two species, daily temperature fluctuations in vegetation gaps broke PY of seeds on the soil surface.

Dormancy break and intraspecific variation. Sara Mira *et al*. studied germination of *Phillyrea angustifolia* (Oleaceae) seeds that are enclosed by a hard (but water-permeable) endocarp. Fruits were collected from six populations on the Iberian Peninsula, and from one population seeds were collected from eight individuals. Seeds were tested for germination and evaluated for morphometric variation. Maternal genetic, as well as environmental, factors influenced

https://doi.org/10.1017/S0960258517000149 Published online by Cambridge University Press

germination and morphometric parameters of the endocarp.

Germination requirements of non-dormant seeds. Geângelo P. Calvi *et al*. found that the recalcitrant seeds of the 'cut-tolerant' species *Eugenia stipitata* (Myrtaceae) germinated when submerged in water. Concentrations of the stress marker antioxidant glutathione (GSH) increased in seeds with submersion time in water. However, seeds that had developed roots and shoots under water had higher concentrations of glutathione disulphide (GSSG) than non-germinated seeds, suggesting that seedlings were less tolerant of flooding than seeds. Furthermore, when the seedlings were detached from seeds, a new 'seedling' was produced.

Germination requirements of non-dormant seeds. Lei Ren *et al*. found that karrikinolide (KAR_1) was present in the smoke water solution made from the burning of prairie hay (*Festuca hallii*) and wheat straw (*Triticum aestivum*) but not alfalfa (*Medicago sativa*). Seed priming in KAR_1 solutions increased germination of *Artemisia frigida*, *Artemisia ludoviciana* and *Conyza canadensis* but not *Cirsium arvense* from the Fescue Prairie in Saskatchewan, Canada. Although KAR_1 was not found in smoke from alfalfa, smoke from this species contained at least one unidentified compound that significantly increased seed germination of *C. canadensis.* Thus, KAR_1 is not present in smoke from all plant species, and Fabaceae may contain important unidentified stimulatory compounds.

Phylogeny and seed traits. Angelino Carta *et al*. conducted a quantitative analysis on published data on the photoinhibition of seed germination (PISG) by white light. Most of the 300 taxa with PISG have dark-coloured seeds and a mass of 1–27 mg, and they are strongly associated with open, disturbed and dry habitats. PISG by white light could result in the formation of a third type of seed bank, i.e. a soil-surface seed bank.

Phylogeny, seed traits and life span. Fabien Arène *et al*. analysed the phylogenetic signal for germination traits and seed size using a worldwide dataset on base temperature and base water potential for germination, seed size, lifespan and climate. They found that base water potential and seed mass should be used to predict moisture niches of plant species, while lifespan, seed size and base temperature should be taken into account in analysing the thermal limits of species distributions.

Pollination. Jerry Baskin and Carol Baskin conducted an extensive literature survey on germination of seeds from chasmogamous (CH, open, potentially outcrossed) *vs* cleistogamous (CL, closed, obligately selfed) flowers. In 252 case studies, CL seeds germinated better in 107 and equally well in 64 (67.9%), and the (CH < CL):(CH > CL) ratio was 107/81 (1.32). These results lend support to the notion that production of CL seeds (which in terms of biomass cost less to produce than CH seeds) by cleistogamous species is advantageous over that of CH seeds. Retention of CH in cleistogamous species may be due to the need to prevent complete selfing, which would lower reproductive success.

Seed dispersal. Alessandra M.O. Santos *et al*. studied seed dispersal effectiveness by birds in two species of *Miconia* (Melastomataceae) from ferruginous *campo rupestre* in Brazil. Fruits were visited by diverse species of birds that differed in quantitative, but not qualitative, seed dispersal effectiveness. The authors concluded that planting of *Miconia* spp. in degraded habitats can overcome seed limitation and promote ecological restoration.

General conclusions

Seed ecology is a highly diverse field of study, and it truly does seek to gain a full understanding of how various biotic and abiotic factors influence every stage in the life of the seed, beginning with flowers and ending with a well-established, healthy seedling. Much progress has been made in each of the traditional subcategories of seed ecology, and now several new combinations of research endeavours have emerged, with more likely to emerge in the future. Seed ecology conferences have contributed greatly to the exchange of ideas and information and to collaborative efforts. Seed Ecology V was highly successful in terms of presentation of new information in each subcategory of seed ecology, including the newly developed ones, and in fostering goodwill and an eagerness to continue communication. Please enjoy this sample of the information presented at Seed Ecology V.