

An Overview of Environmental Cues That Affect Germination of Nondormant Seeds

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Abstract: For a successful germination and plant growth, seeds must germinate at the right time. Seeds must become nondormant and must fulfill the seed germination requirements. These requirements include light/dark, moisture, temperature, and other environmental cues (e.g., ethylene, exudate from host roots, or chemicals from fire) in the habitat. Seeds come out from dormancy in response to environmental cues, but depending on the species, they may need to be exposed to a second set of environmental cue to germinate. That is, nondormant seeds require specific temperature and water conditions to germination, and sometimes unfavorable temperature and water conditions will cause seeds to enter secondary dormancy. There are still mysteries about how/what environmental cues help seeds detect the right time/conditions for germination after dormancy is broken. Our knowledge of species-specific conditions is incomplete and further studies are needed.

Keywords: chemical compounds; fire; light; temperature; water potential



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1. Introduction

It has been at least 350 million years since the first ovule was produced by plants (*Elkinsia*), and this was an early major development in the long sequence of changes resulting in seeds of gymnosperms and eventually angiosperms. Along with changes in seed morphology and the way nutrients are provided for the embryo, i.e., female gametophyte and endosperm in gymnosperms and angiosperms, respectively, seed dormancy has evolved, which plays an important role in controlling the timing of germination in nature. That is, seed dormancy is a part of the adaptations of a plant species that delay germination until environmental conditions are favorable for seedling survival and growth. Further, if seeds germinate at the beginning of the favorable period for plant growth, seedlings have the whole period in which to grow and become established. The timing of germination is controlled by two factors: seeds have to become nondormant and the germination requirements of the nondormant seeds must be fulfilled, e.g., light/dark, moisture, temperature, and other environmental cues such as ethylene, exudate from host roots, or chemicals from fire are present in the habitat.

There may be variability in the degree of dormancy between the seeds from the same population, plant, or individual inflorescence due to genetics, environmental effects on the mother plant, or genetics × environment interactions. Thus, diaspores can vary continuously in size, mass, shape, color, and dormancy-breaking and germination requirements [1]. In diaspore heteromorphic species, the diaspores produced by the same plant exhibit distinct differences, including size/mass of the embryo, pericarp thickness, level of dormancy, dispersal ability, and ability to form persistent seed banks [1]. Thus, in considering the

germination of seeds, it is important to understand that the seeds of a particular species may differ in their responses to environmental cues.

There are still mysteries about how/what environmental cues help seeds detect the right time/conditions for germination after dormancy is broken. Thus, the purpose and scope of this special issue is to encourage the publication of review and/or experimental studies on ecology, physiology, biochemistry, and molecular biology related to the effect of environmental cues on the promotion/timing of seed germination.

2. Temperature

There are two ways in which seasonal temperature changes affect germination. First, dormant seeds require exposure to specific temperature regimes for dormancy-break to occur, assuming that adequate soil moisture is present. Seeds with a physiological-inhibiting mechanism of germination, i.e., physiological dormancy (PD), require high summer temperatures (known as warm stratification or after-ripening) and/or low winter temperatures (known as cold stratification), depending on the species, for dormancy-break to occur. There are three levels of PD: nondeep, intermediate, and deep. Seeds with nondeep (and sometimes intermediate) PD may become nondormant at one temperature but not germinate until they are exposed to other temperatures. For example, if dormancy-break occurs in summer, low temperatures of autumn promote germination, but if dormancy-break occurs in winter, high temperatures of spring/summer promote germination. Seeds with deep PD may germinate at the temperature at which dormancy-break occurs. In the case of seeds with a water-impermeable seed/fruit coat (i.e., physical dormancy), seeds may become sensitive to dormancy-break at high or low temperatures, and then the water gap opens (dormancy-break) when seeds are exposed to a low or high temperature, respectively [1].

Second, nondormant seeds will germinate at a certain range of temperatures, described by the cardinal temperatures, which differ between species and even among genotypes within a species [2,3]. The temperature below which seeds will not germinate is the base temperature. Temperatures above which seeds will not germinate is the ceiling temperature. The temperature(s) at which germination occur(s) at its maximum rate and percentage is the optimum temperature(s).

Some seeds with nondeep PD have been shown to germinate over a narrow range of temperatures when their degree of dormancy is high, and they germinate over a broader range of temperatures as dormancy is broken [4–6]. For nondormant seeds, the temperature window for germination corresponds to the cardinal temperatures. There are six types of nondeep PD, and the decrease in dormancy occurs with the change in the seasons [1,7]. In other words, by receiving appropriate environmental cues (temperature changes during the seasons), seeds can be in one of the three states: complete dormancy, conditional dormancy (only in Types 1, 2, and 3), or no dormancy. Seeds germinate when the temperature requirement for germination overlaps with habitat temperatures, if the soil is moist. Seeds of warm-season species become nondormant during winter, and the increasing temperatures in spring promote germination. On the other hand, seeds of cool-season species become nondormant in summer, and the decreasing temperatures in autumn promote germination.

3. Water

Water is required for seeds to germinate. Seeds cannot absorb water if the water potential of the germination medium is less (more negative) than the threshold for germination [8]. This threshold is called the base water potential for germination, and the base water potential for germination percentiles are different (higher at lower percentiles and lower at upper percentiles) and usually follow a normal distribution in a seed population. In the seed population, the median value of the base potential is known as the base potential [8,9].

It is possible to alter the basal water potential for germination in a population of seeds with PD [10]. High levels of PD result in a high basal water potential; however, the removal of PD reduces that potential and seeds can germinate in soils with a low moisture content. Thus, a lack of water may inhibit germination due to seed dormancy or a higher

base water potential. On the other hand, drought can induce secondary dormancy in seeds; that is, seeds can enter secondary dormancy after being exposed to drought stress for a long period of time [6]. Hence, the water cue is effective in controlling the timing of germination of all seeds through the base water potential for germination, which can change as dormancy-break or dormancy-induction occurs in nature.

Seeds are affected by waterlogging due to low levels of oxygen and the production of ethylene in soils (see Section 6). When seeds are waterlogged for a short period of time, the starch content is lowered but the sugar-soluble content is increased as the starch in the seeds can be directly converted to soluble sugar [11,12]. A high level of soluble sugars in seeds can facilitate germination, particularly when starch is the major storage material [12]. However, long-term flooding leads to reduced protein, starch, and soluble sugar content in the seeds as a result of physiological changes associated with hypoxia [11,12]. When seeds are flooded for a long period of time, however, they experience hypoxia, which results in low energy consumption for aerobic respiration and high energy consumption for anaerobic respiration [11]. Seeds of various species can tolerate waterlogging for varying lengths of time; however, they do not germinate until waterlogging ends [1]. Generally, germination of most seeds is stimulated by a short period of waterlogging, whereas prolonged waterlogging causes the ground to become anaerobic, which results in a delay in germination or seed death [11]. Nondormant seeds of some species such as *Scirpus hallii* require flooding, i.e., ethylene, and light to germinate [13].

4. Light

Despite the high percentages of seeds that germinate at both light and darkness [1], depending on the species, some seeds germinate only in light [14,15] and others only in darkness [16]. Seeds that germinate when exposed to light are called positively photoblastic, while negatively photoblastic seeds are inhibited by light. There is a major difference in opinion regarding what exposure to light does with regard to promoting germination. In addition, seeds of some species require light at one temperature but not at other temperatures, e.g., seeds of *Lactuca sativa* require light at high temperatures but not at low temperatures [17]. Molecular biologists think light suppresses the last genes that inhibit germination, i.e., it breaks the last part of dormancy [18–20]. Seed ecologists think light is one of the environmental signals that can promote germination after dormancy has been broken [21].

The phytochrome-regulated production of gibberellin appears to be responsible for the response to light. By absorbing red light, a phytochrome is converted from its inactive Pr (which inhibits germination) to its active Pfr form (which promotes germination) [22]. In contrast, far-red light converts Pfr into Pr [22]. It is important to keep in mind that some seeds germinate better under far-red than red light. There are three modes of phytochrome action in seeds [23]: (1) very low fluence response (VLFR), (2) low fluence response (LFR), and (3) high irradiance response. It may depend on the species or sometimes the degree of seed dormancy whether VLFR or LFR promotes germination [24]. Seeds of some species, however, do not respond to a single light exposure, and they require repeated exposures to light before germinating [25,26]. Five different phytochromes have been identified in *Arabidopsis thaliana*, and they are identified as phytochrome A, B, C, D, and E and are sensitive to different fluences of light [1].

5. Fire

In fire-prone ecosystems, fire (high temperatures and smoke) can be a cue that breaks the dormancy of seeds by opening the water gap on the seed coat [27], and germination occurs in an open canopy without competition. Smoke contains chemical compounds (such as karrikinolide) capable of stimulating germination in seeds from a wide range of plant families, growing in both fire-prone and nonfire-prone ecosystems [1]. Various species with PD have been evaluated for the effect of smoke on germination, and in some cases,

germination has been improved by the smoke [28–30]. However, smoke may inhibit seed germination in some species or induce dormancy [1].

6. Chemical Compounds

Many inorganic ions have been investigated with regard to their effects on seed germination. However, only nitrogen (N)-containing compounds (e.g., nitrate and nitrite) have been shown to have a significant impact on germination [1]. The promotive effects of nitrate on germination may be increased by interaction with light and temperature. A nitrate-containing fertilizer can stimulate weed seed germination in arable lands [31]. A number of sources, however, have been cited in Baskin and Baskin [1] showing that N-containing compounds do not improve weed germination. Many seeds need both N-containing compounds and light as a cue to germination; thus, nitrate fertilizers may not be efficient in stimulating germination if seeds are in the soil.

The soil contains chemical organic compounds produced by plant materials, soil organisms, and animal feces, which are capable of stimulating or inhibiting germination, thus influencing the timing of germination. Various volatile hydrocarbons found in soils, including ethylene and propylene, stimulate germination. Seed ecologists are particularly interested in ethylene as its presence in soil air can reach 18 ppmv, which is high enough to promote seed germination. However, ethylene does not stimulate all seeds to germinate, and the germination of some seeds is inhibited by it [1].

In agricultural soils, pesticides and herbicides produced from organic compounds are deliberately applied, which may affect the germination of weed seeds. Germination may be increased, decreased, or unaffected depending on the herbicide used and the plant species [1]. However, the effects of herbicides on seed germination vary with the method of herbicide application, the concentration, the length of exposure, and the temperature during seed exposure to the compound(s). Herbicides have been widely used, and this has resulted in weeds developing herbicide resistance, which changes their germination requirements [32]. For example, seeds of herbicide-resistant *Avena sterilis* ssp. *ludoviciana* biotypes had higher base water potentials than the susceptible biotype and thus required more water to germinate [33].

Salinity per se does not act as an environmental cue in the seeds to initiate germination, but decreases in salinity with the onset of rain can stimulate germination. Both halophytes and nonhalophytes germinate better under nonsaline than in saline conditions [1]. Further, if high salinity inhibits the germination of halophytes, seeds will germinate when the salinity is lowered. Soil pH can affect seed germination, and the seeds of many plant species have a favorable range of pH for germination. The optimum pH for germination is 6.5 to 7, but there are exceptions [1].

7. Conclusions

Seeds come out from dormancy in response to environmental cues, but depending on the species, they may need to be exposed to a second set of environmental cues to germinate. That is, nondormant seeds require specific temperature and water conditions for germination, and sometimes unfavorable temperature and water conditions will cause seeds to enter secondary dormancy. However, for many species, other environmental factors such as organic and inorganic chemicals may also play a role in the timing of germination. Our knowledge of species-specific conditions is incomplete and further studies are needed.

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