



Seed dormancy in alpine species

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ARTICLE INFO

Article history:

Received 21 December 2010

Accepted 14 February 2011

Keywords:

Cold-dry seed storage
Cold-wet seed storage
Dormancy classification
Embryo morphology
Light response
Scarification

ABSTRACT

In alpine species the classification of the various mechanisms underlying seed dormancy has been rather questionable and controversial. Thus, we investigated 28 alpine species to evaluate the prevailing types of dormancy. Embryo type and water impermeability of seed coats gave an indication of the potential seed dormancy class. To ascertain the actual dormancy class and level, we performed germination experiments comparing the behavior of seeds without storage, after cold-dry storage, after cold-wet storage, and scarification. We also tested the light requirement for germination in some species. Germination behavior was characterized using the final germination percentage and the mean germination time. Considering the effects of the pretreatments, a refined classification of the prevailing dormancy types was constructed based on the results of our pretreatments. Only two out of the 28 species that we evaluated had predominantly non-dormant seeds. Physiological dormancy was prevalent in 20 species, with deep physiological dormancy being the most abundant, followed by non-deep and intermediate physiological dormancy. Seeds of four species with underdeveloped embryos were assigned to the morphophysiological dormancy class. An impermeable seed coat was identified in two species, with no additional physiological germination block. We defined these species as having physical dormancy. Light promoted the germination of seeds without storage in all but one species with physiological dormancy. In species with physical dormancy, light responses were of minor importance. We discuss our new classification in the context of former germination studies and draw implications for the timing of germination in the field.

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Introduction

A dormant seed was defined by Baskin and Baskin (2004a) as 'one that does not have the capacity to germinate in a specified period of time under any combination of normal physical environmental factors (temperature, light/dark, and so forth)' that would otherwise be favorable for the germination of non-dormant seeds (ND). Dormancy is an innate mechanism of seeds that is determined

by both the morphological and physiological properties of the seed (Finch-Savage and Leubner-Metzger, 2006), whereas the release of dormancy is triggered by environmental stimuli (Baskin and Baskin, 1998; Benech-Arnold et al., 2000; Fenner and Thompson, 2005; Finch-Savage and Leubner-Metzger, 2006; Vleeshouwers et al., 1995).

The study of these commonly accepted phenomena led to the comprehensive hierarchical system of seed dormancy classification proposed by Baskin and Baskin (1998, 2004a,b). It distinguishes five classes: (1) physiological dormancy (PD), (2) morphological dormancy (MD), (3) morphophysiological dormancy (MPD), (4) physical dormancy (PY), and (5) a combinational dormancy (PY + PD). Although endogenous and exogenous factors are responsible for the maintenance or release of dormancy (Baskin and Baskin, 1998, 2004a; Benech-Arnold et al., 2000; Fenner and Thompson, 2005; Finch-Savage and Leubner-Metzger, 2006; Vleeshouwers et al., 1995), a feasible key for the determination of dormancy status based on embryo morphology, the seed coat's permeability to water, and the capacity of fresh seeds to germinate within one month is available (Baskin and Baskin, 2004b).

Various physiological mechanisms, which may be present in the embryo itself and/or in surrounding structures, were reported to inhibit radicle emergence, all of which are classified as PD (reviewed in Finch-Savage and Leubner-Metzger, 2006). Three levels of dormancy are distinguished within PD (Baskin and Baskin,

Abbreviations: CDS_{fresh}, cold-dry storage of seeds before incubation under long-day conditions; CDS_{sc}, scarification of seeds following cold-dry storage before incubation under long-day conditions; CWS_{fresh}, cold-wet storage of seeds before incubation under long-day conditions; CWS_{subs}, cold-wet storage subsequent to a germination experiment before incubation under long-day conditions; FGP, final germination percentage; FRESH_{dark}, seeds without storage incubated in darkness; FRESH_{sc}, scarification of seeds without storage before incubation under long-day conditions; FRESH_{LD}, seeds without storage incubated under long-day conditions; GA3, gibberellic acid; MD, morphological dormancy; MGT, mean germination time; MPD, morphophysiological dormancy; ND, non-dormant; PD, physiological dormancy; PY, physical dormancy; PY + PD, combinational dormancy of PY and PD.

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1998, 2004a,b): non-deep, intermediate, and deep dormancy. Temperature is the main driving factor that releases or induces PD (Baskin and Baskin, 2004a; Vleeshouwers et al., 1995), although other environmental factors such as naturally occurring chemical signals may have roles as well (Finch-Savage and Leubner-Metzger, 2006). Therefore, exposing seeds to certain temperatures may provide an indication of the type of dormancy exhibited by a species (Baskin and Baskin, 2004b). Seeds with non-deep PD are released from dormancy, often at a slow rate, when they are stored dry at room temperature. This phenomenon is called 'after-ripening' (Finch-Savage and Leubner-Metzger, 2006), and this transitional stage was termed conditional dormancy by Baskin and Baskin (1998). Release from non-deep PD may occur also during dry-cold storage (Wang et al., 2010). Seeds with intermediate PD often require two to three months of cold stratification, i.e., storage under temperatures below 10 °C in an imbibed stage, to overcome dormancy, whereas seeds with a deep PD are released of dormancy only after longer periods of cold stratification (Baskin and Baskin, 1998, 2004b). Dormancy induced by the underdevelopment of embryos (i.e., in MD and MPD) requires a short period of favorable conditions for the embryo to grow to a species-specific critical size (Baskin and Baskin, 1998, 2004b; Finch-Savage and Leubner-Metzger, 2006). In MPD, an additional physiological component is involved (Baskin and Baskin, 1998). Seeds with PY or PY + PD remain dormant until something disintegrates the covering layers, which are otherwise impermeable to water (Baskin et al., 2000).

Whether light plays a role in the release of dormancy or merely promotes germination has been the subject of some debate (Baskin and Baskin, 2004a; Benech-Arnold et al., 2000; Fenner and Thompson, 2005; Finch-Savage and Leubner-Metzger, 2006; Pons, 2000; Vleeshouwers et al., 1995). Independent of the criteria used to determine when dormancy ends and germination begins, light affects germination in many species in the field (Pons, 2000). In the investigations reported here we considered light as an environmental cue that may influence germination in non-dormant seeds (Baskin and Baskin, 2004a).

In alpine species, dormancy is a long recognized phenomenon. As early as 1913, Braun had already reported that many species did not germinate at all under laboratory conditions, even after cold stratification. Other pioneer studies suggested that most alpine species are non-dormant (Amen, 1966). Low germination success of some alpine plants challenged botanists and growers of ornamental plants for decades (Favarger, 1953). In more recent reviews, Baskin and Baskin (1998, 2004b) reported that >70% of arctic-alpine species have dormant seeds, exhibiting mainly PD or, to a much lesser extent, PY. Despite some early comprehensive studies on seed germination in alpine environments in the beginning of the 20th century (reviewed in Körner, 2003) and Amen's early overview on seed dormancy in alpine plants (1966), there is still a lack of knowledge of the mechanisms that underlie dormancy in alpine species (Baskin and Baskin, 1998).

The goal of this study was to reconsider the types of dormancy exhibited by 28 species of alpine plants in light of the classification system proposed by Baskin and Baskin (1998, 2004a,b). We first considered embryo type and the water impermeability of seed coats, to determine the potential classes of seed dormancy. Furthermore, we applied several germination experiments comparing the germination of freshly collected seeds with germination following various pretreatments. Additionally, the light requirements for the germination of some species were tested. Germination behavior was characterized by final germination percentage (FGP) and mean germination time (MGT). With the data generated by our germination experiments, we refined the classification of dormancy types. According to Baskin and Baskin (1998), several alpine species previously classified as exhibiting ND may actually have PD. Based on that suggestion, we hypothesized that the majority of fresh seeds of

our investigated species are dormant, i.e., few mature seeds would germinate readily within one month and without any pretreatments. More specifically, we asked which types of dormancy can be found in the alpine species and what preconditions do they require for overcoming dormancy. Furthermore, we hypothesized that light promotes germination in alpine species, as they should be adapted to the pronounced seasonal patterns of the light environment in the mainly open vegetation types.

Materials and methods

Study site and species

Seeds were collected in the Rotmoos Valley (11°02'E/46°49'N), a glacial valley in the central Alps of Austria. For a detailed description of the vegetation, see Raffl et al. (2006). Seeds were collected at altitudes ranging from 2250 to 3000 m.

We investigated 28 alpine species, representing 14 families (Table 1). The investigated species include some of the most abundant species in glacier forelands, such as *Anthyllis alpicola*, *Poa alpina*, *Trifolium pallescens*, *Saxifraga aizoides* and *S. oppositifolia* (Raffl et al., 2006) and some species occurring frequently on the adjacent slopes (*Potentilla aurea*, *P. frigida*, *Ranunculus glacialis*). Fully ripened seeds or fruits were collected in the late summer and autumn from 2000 to 2010 (see Appendix A). For simplicity, the term 'seed' is used to describe both seeds and fruits. Seeds were collected from randomly chosen individuals (mostly >50 individuals per species). They were mixed thoroughly to minimize the effects of single individuals on germination. Immediately after collection, the seeds were stored in a commercial refrigerator at 4 °C until the start of the pretreatments or germination experiments (Table 1).

Potential dormancy classes

Based on embryo morphology and the impermeability of the seed coat to water (Baskin and Baskin, 2004b), we assigned each species to one of the following potential seed dormancy classes (including ND): species with a water-impermeable seed coat (PY/PY + PD); species with a water-permeable seed coat and underdeveloped embryos (MD/MPD); species with a water-permeable seed coat and fully developed embryos (ND/PD). For the determination of the embryo type, we used the key provided by Baskin and Baskin (2007). Information on embryo and endosperm structures was available from studies by Martin (1946) and other authors (Akhalkatsi and Wagner, 1997; Baskin and Baskin, 2005; Wagner and Teng, 1993; Wagner et al., 2010). For some species, we inferred embryo type from a reference species, i.e., a related taxon, as 'their basic internal organization varies only slightly among related species and genera' (Martin, 1946). We assumed a water-impermeable seed coat for those species belonging to families for which evidence of physical dormancy has been reported (Baskin et al., 2000).

Preconditions

Germination experiments with different preconditions were conducted over several years (Table 1). Germination of fresh seeds without storage under long-day conditions was tested for all investigated species (FRESH_{LD}), whereas the germination without storage in darkness (FRESH_{dark}) was measured for only a subset (Table 1). Seeds without storage were tested within one week of seed collection.

To test the effects of cold storage, the samples were placed in a commercial refrigerator at 4 °C. For cold-dry storage (CDS_{fresh}), fresh seeds were placed, respectively, either in dry paper bags for

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