**Germination ecology in alpine species**

Seed germination is an essential, yet most vulnerable stage of the plant life cycle (Fenner and Thompson 2005). Because it is an irreversible physiological process, it must be timed to occur when the environment is favourable for subsequent seedling establishment (Poschlod et al., 2013). Consequently, many plant species have developed seed dormancy states in which germination is prevented during periods that are only ephemerally favourable (Willis et al. 2014); different degrees of dormancy also ensure the distribution of the offspring across time, as bet-hedge against unpredictably variable environments (Jurado and Flores 2005; Venable, 2007). Across species, germination and dormancy patterns are primary affected by a combination of genetic and environmental factors (Baskin and Baskin 2014), such as phylogeny (Nikolaeva, 1977, 1999; Figueroa and Armesto, 2001), seed mass (Schwienbacher and Erschbamer 2002; Bu et al. 2007; Liu et al. 2013) and climate (Willis et al. 2014), including environmental-induced maternal effects (Donohue et al., 2005; Bernareggi et al. 2016). Because seeds must first be able to germinate and establish in a habitat, germination and dormancy traits are major determinants of species’ distributions (Donohue et al., 2010; Jimenez-Alfaro et al. 2016; Fraaije et al. 2015); accordingly, differences in germination traits have been attributed to habitat preference (Carta et al. 2016; Tudela-Isanta et al. 2018b) and chorology (*sensu* Passalacqua 2015; Orsenigo et al. 2015 ; Tudela et al. 2018a; Giménez-Benavides, et al. 2005).

In the alpine environment, the large taxonomic and habitats diversity resulted in high variable germination traits across species, which makes it difficult to define a common “alpine” germination strategy. Early studies on germination ecology of alpine plants demonstrated that freshly collected seeds of most arctic and alpine species required relatively high temperatures for germination (Bliss, 1958; Amen, 1966, Billings and Mooney, 1968). The requirement of high temperatures for germination has been considered an adaptation to prevent seed germination at the timing of seed dispersal (autumn), when temperatures are low and there is a high risk of frost (Cavieres and Arroyo, 2000). Indeed, seed germination of alpine species tends to occur after exposure to winter in early summer (Korner, 2003; Mondoni et al. 2015); at this stage the temperature window for germination usually widens toward lower values (Baskin and Baskin, 2014). Nevertheless, there is an increasing number of studies highlighting the germination of freshly collected seeds at cool incubation temperatures or even under cold stratification treatments (Schwienbacher et al. 2011; Hoyle et al. 2015; Fernández-Pascual et al. 2017). The requirements of low temperatures for germination has been considered an adaptation which presumably ensure seedlings to reach a deeper root system before topsoil desiccation in summer (Kammer and Mohl, 2016) and an optimal size for overwintering (Billings and Mooney 1968).

The influence of the environmental conditions as driver of these contrasting germination responses to temperature is gaining recognition. For example, alpine species show higher optimal temperature for germination in than either subalpine species (i.e. species that live close to the treeline, Fernández-Pascual et al. 2017) or their congeneric counterpart at below the treeline (Walder and Erschbamer 2015).

Differences in germination traits have been attributed also to species’ successional niche and habitat preferences, with pioneer species germinating better at colder temperatures than later successional species (Schwienbacher, et al. 2012), while species from calcareous and siliceous alpine grasslands showing a slow, mostly overwinter germination and high germination under all conditions, respectively (Tudela-Isanta et al. 2018ab). Nevertheless, no habitat-related germination strategies were identified when comparing fellfield and snowbed habitats (Shimono and Kudo 2005).

Unlike the response to temperature, seed germination of alpine species seems tightly controlled by dormancy and light, with most species being physiologically dormant (Baskin & Baskin, 2014; Schwienbacher et al., 2011; Sommerville et al., 2013) and requiring light for germination (Jaganathan et al., 2015), though some trend exist (see e.g. Sommerville et al., 2013 Giménez-Benavides, et al. 2005). Both traits are thought to provide some advantage in establishing persistent seed banks in temporally and spatially unpredictable alpine environments (Cavieres 1999 and Cavieres and Arroyo 2001), preventing germination in late autumn and shifting it to spring (Densmore, [1997](https://link.springer.com/article/10.1007/s12229-014-9150-2#ref-CR47); Jaganathan et al., 2015).

Therefore, current evidences suggest that fresh seeds of alpine species are dormant and require light for germination. Conversely, germination response to temperature show higher variability across alpine taxa, depending mostly on elevation and habitat conditions. These traits play a pivotal role in controlling the timing of seedling emergence in alpine environments.

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In the alpine environment, the large species and microhabitats diversity coupled with a spatially variable and temporally unpredictable climatic conditions have resulted in a variety of germination responses and dormancy types, which makes it difficult to define a common “alpine” germination strategy (Hoyle et al., 2015; Körner, 2003; Schwienbacher, et al., 2011). For example, although many alpine plants have deep physiological dormancy (Baskin & Baskin, 2014; Schwienbacher et al., 2011; Sommerville, et al, 2013) and require light (Jaganathan et al., 2015) and high temperatures for germination (Jumpponen, et al, 1999), nondormant seeds (Sommerville et al., 2013), very low temperature requirements and dark conditions (Schwienbacher et al., 2011) for germination have also been observed. In this regard, differences in germination traits have been attributed to slope orientation (Xu, et al. 2017), biogeographical provenance (Giménez-Benavides, et al. 2005), species’ successional niche (Schwienbacher, et al. 2012) and habitat preferences (Tudela et al. 2018).