**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). Thus, the mechanisms regulating the timing of this transition are expected to be under strong selective pressure (Angevine and Chabot, 1979; Willis et al., 2014). Consequently, natural selection should favour seed germination requirements that reduce the probability of facing environmental conditions that are not appropriate for seedlings establishment (Willis et al., 2014; Baskin and Baskin, 2014). 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).

Alpine environments are those that occur above the natural elevation where tree can grow, and are characterized by low temperatures, strong winds, unstable substrates, and short growing seasons (Körner, 2003). The short growing season of alpine habitats is a major barrier for plants recruitment as it constrains seedlings growth and the period favorable for their establishment (Chambers et al., 1990; Forbis, 2003) because seedlings have to attain a critical biomass by the end of growing season to withstand the harsh and long-lasting winter conditions (Schütz, 2002).

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; Cavieres and Sierra-Almeida, 2018). 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 requirement of a cold stratification period for germination in alpine species would allow seeds to sense the presence of snow, thereby timing the germination to a period appropriate for seedling survival and establishment. This way, cold stratification requirements would prevent precocious germination under autumn conditions where appropriate soil moisture and temperatures to complete seed germination and seedling establishment are not likely to persist for more than a few days (Meyer and Monsen, 1991). Thus, it may be expected that a cold stratification period would be a common requirement for seed germination in alpine plant species. In an early review, Amen (1966) concluded that cold stratification was not a common requirement for the seed germination of several alpine plant species from different mountains in the USA (see also Sayers and Ward, 1966; Marchand and Roach, 1980; Kaye 1997). More recently, Sommerville et al. (2013) and Hoyle et al. (2015) showed that in 19 and 54 Australian alpine plant species, respectively, a cold stratification period significantly increased seed germination only in half of the species tested. In contrast, Söyrinki (1938, cited in Körner 2003) experimenting with 91 alpine species from the Alps, found that storage at winter temperatures (cold stratification) increased seed germination in the great majority of species. Shimono and Kudo (2005) reported that cold stratification increased the seed germination over a range of temperatures in most of the 27 plant species studied in the alpine zone of Japan. Cavieres and Sierra-Almeida (2018) reported that along an elevational gradient in the central Chilean Andes cold stratification was an important requirement for seed germination in species from lower elevations, whilst species from higher elevations required other factors than cold-stratification to break seed dormancy. Therefore, how important is cold stratification for seed germination in alpine plant species remains elusive and require global assessments.

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.

**Reference**

Amen R.D. (1966). The extent and role of seed dormancy in alpine plants. The Quarterly Review of Biology 41: 271–281.

Angevine, M.W., Chabot, B. F., 1979. Seed germination syndromes in higher plants, in: Solbrig, O.T., Jain, S., Johnson, G.B, Raven, P. (Eds.), Topics in Plant Population Biology. Columbia University Press, New York, pp, 188−206.Baskin, C. C., Baskin, J. M. (2014). Seeds: Ecology, biogeography, and evolution of dormancy and germination (2nd ed.). London: Academic Press.

Billings, W. D., Mooney, H. A. (1968). The ecology of arctic and alpinecplants. Biological Review, 43, 481–529. https://doi.org/10.1111/brv.1968.43.issue-4

Bliss LC. 1958. Seed germination in arctic and alpine species. Arctic 11:180–188.

Cavieres LA, Arroyo MTK. 2000. Seed germination response to cold stratification period and thermal regime in Phacelia secunda (Hydrophyllaceae): altitudinal variation in the Mediterranean Andes of Central Chile. Plant Ecology 149: 1–8.

Cavieres, L. A., Sierra-Almeida, A. (2018). Assessing the importance of cold-stratification for seed germination in alpine plant species of the High-Andes of central Chile. Perspectives in Plant Ecology, Evolution and Systematics, 30, 125-131.

Chambers, J.C., MacMahon, J.A., Brown, R.W., 1990. Alpine seedling establishment: the influence of disturbance type. Ecology 71, 1323−1341.

Donohue K, Dorn L, Griffith C, Kim E, Aguilera A, Chandra R, Schmitt J. 2005. Niche construction through germination cueing: life-history responses to timing of germination in Arabidopsis thaliana. Evolution 59: 771–785

Donohue K, Rubio de Casas R, Burghardt L, Kovach K, Willis CG. 2010. Germination, postgermination adaptation, and species ecological ranges. Annual Review of Ecology, Evolution and Systematics 41: 293–319

Fenner M, Thompson K. 2005. The ecology of seeds. Cambridge: Cambridge University Press.

Fernández-Pascual, E., Jiménez-Alfaro, B., & Bueno, Á. 2017. Comparative seed germination traits in alpine and subalpine grasslands: Higher elevations are associated with warmer germination temperatures. Plant Biology, 19, 1–9. https://doi.org/10.1111/plb.12472

Figueroa A, Armesto J.J. 2001. Community-wide germination strategies in a temperate rainforest of Southern Chile: ecological and evolutionary correlates. Aust. J. Bot., 49: 411-425

Fraaije, R. G., ter Braak, C. J., Verduyn, B., Breeman, L. B., Verhoeven, J. T., and Soons, M. B. (2015). Early plant recruitment stages set the template for the development of vegetation patterns along a hydrological gradient. Functional Ecology, 29(7), 971-980.

Forbis, T.A., 2003: Seedling demography in an alpine ecosystem. Am. J. Bot. 90, 1197−1206.

Giménez-Benavides, L., Escudero, A., & Pérez-García, F. 2005. Seed germination of high mountain Mediterranean species: Altitudinal, interpopulation and interannual variability. Ecological Research, 20, 433–444. <https://doi.org/10.1007/s11284-005-0059-4>

Hoyle, G. L., Steadman, K. J., Good, R. B., McIntosh, E. J., Galea, L. M. E., & Nicotra, A. B. 2015. Seed germination strategies: An evolutionary trajectory independent of vegetative functional traits. Frontiers in Plant Science, 6, 1–13. <https://doi.org/10.3389/fpls.2015.00731>

Jaganathan, G. K., Dalrymple, S. E., Liu, B. 2015. Towards an understanding of factors controlling seed bank composition and longevity in the alpine environment. The Botanical Review, 81, 70–103. https://doi.

Jiménez-Alfaro, B., Silveira, F. A. O., Fidelis, A., Poschlod, P., & Commander, L. E. 2016. Seed germination traits can contribute better to plant community ecology. Journal of Vegetation Science, 27, 637–645. <https://doi>. org/10.1111/jvs.12375

Jurado, E. & J. Flores. 2005. Is seed dormancy under environmental control or bound to plant traits? Journal of Vegetation Science 16: 559–564.

Jumpponen, A., Vare, H., Mattson, K. G., Ohtonen, R., & Trappe, J. M. 1999. Characterization of “safe sites” for pioneers in primary succession on recently deglaciated terrain. Journal of Ecology, 87, 98–105. https://doi.org/10.1046/j.1365-2745.1999.00328.x

Kammer, P. M., Mohl, A. 2016. Factors controlling species richness in alpine plant communities: An assessment of the importance of stress and disturbance. Arctic, Antarctic, and Alpine Research, 34(4), 398–407. <https://doi.org/10.2307/1552197>

Kaye, T. 1997. Seed dormancy in high elevation plants: implications for ecology and restoration. In Kaye, T.N., Liston, A., Love, R.M., Luoma, D.L., Meinke, R.J., Wilson, M.V. (Eds). Conservation and Management of Native Plants and Fungi. Native Plant Society of Oregon, Corvallis, Oregon. Pages 115−120.

Körner, C. (2003). Alpine plant life. Berlin, Heidelberg: Springer Berlin Heidelberg. <https://doi.org/10.1007/978-3-642-18970-8>

Marchand, P.J., Roach, D.A., 1980. Reproductive strategies of pioneering alpine species: seed production, dispersal and germination. Arctic Alpine Res. 12, 137−146.Marcante, S., Sierra-Almeida, A., Spindelböck, J. P., Erschbamer, B., & Neuner, G. (2012). Frost as a limiting factor for recruitment and establishment of early development stages in an alpine glacier foreland? Journal of Vegetation Science, 23, 858–868. https://doi.org/10.1111/jvs.2012.23.issue-5

Meyer, S.E., Monsen, S.B., 1991. Habitat-correlated variation in mountain big sagebrush (Artemisia tridentata ssp. vaseyana) seed germination patterns. Ecology 72, 739−742.

Nikolaeva, M. G. (1977). Factors controlling the seed dormancy pattern. Physiology and Biochemistry of Seed dormancy and Germination.

Nikolaeva, M. G. (1999). Patterns of seed dormancy and germination as related to plant phylogeny and ecological and geographical conditions of their habitats. Russian Journal of Plant Physiology, 46, 369-373.

Orsenigo, S., Abeli, T., Rossi, G., Bonasoni, P., Pasquaretta, C., Gandini, M., & Mondoni, A. (2015). Effects of autumn and spring heat waves on seed germination of high mountain plants. PLoS One, 10, 1–17. <https://doi.org/10.1371/journal.pone.0133626>

Passalacqua, N. G. (2015). On the definition of element, chorotype and component in biogeography. Journal of Biogeography, 42, 611–618. <https://doi.org/10.1111/jbi.2015.42.issue-4>

Poschlod, P., Abedi, M., Bartelheimer, M., Drobnik, J., Rosbakh, S., & Saatkamp, A. (2013). Seed ecology and assembly rules in plant communities. In E. Van der Maarel & J. Franklin (Eds.), Vegetation ecology (2nd ed., pp. 164–202). Oxford: John Wiley & Sons. <https://doi>.

Sayers, R.L., Ward, R.T., 1966. Germination responses in alpine species. Bot. Gaz. 127, 11−16.

Schwienbacher E, Navarro-Cano JA, Neuner G, Erschbamer B (2012) Correspondence of seed traits with niche position in glacier foreland succession. Plant Ecol 213:371–382. <https://doi.org/10.1007/s11258-011-9981-4>.

Schwienbacher, E., Navarro-Cano, J. A., Neuner, G., & Erschbamer, B. (2011). Seed dormancy in alpine species. Flora: Morphology, Distribution, Functional Ecology of Plants, 206, 845–856. <https://doi.org/10.1016/j.flora.2011.05.001>

Shimono, Y., & Kudo, G. (2005). Comparisons of germination traits of alpine plants between fellfield and snowbed habitats. Ecological Research, 20, 189–197. <https://doi.org/10.1007/s11284-004-0031-8>

Sommerville, K. D., Martyn, A. J., & Offord, C. (2013). Can seed characteristics or species distribution be used to predict the stratification requirements of herbs in the Australian Alps? Botanical Journal of the Linnean Society, 172, 187–204. <https://doi.org/10.1111/boj.12021>

Tudela‑Isanta M., Ladouceur E., Wijayasinghe M., Pritchard H.W., Mondoni A. (2018)b The seed germination niche limits the distribution of some plant species in calcareous or siliceous alpine bedrocks. Alpine Botany 128: 83–95. <https://doi.org/10.1007/s00035-018-0199-0>

Tudela‐Isanta, M., Fernández‐Pascual, E., Wijayasinghe, M., Orsenigo, S., Rossi, G., Pritchard, H. W., & Mondoni, A. (2018)a. Habitat‐related seed germination traits in alpine habitats. Ecology and Evolution, 8, 150–161. https ://doi.org/10.1002/ece3.3539

Venable DL. 2007. Bet hedging in a guild of desert annuals. Ecology 88: 1086–1090.

Walder T, Erschbamer B (2015) Temperature and drought drive differences in germination responses between congeneric species along altitudinal gradients. Plant Ecology

Willis, C. G., Baskin, C. C., Baskin, J. M., Auld, J. R., Venable, D. L., Cavender-Bares, J., … Wilczek, A. (2014). The evolution of seed dormancy: Environmental cues, evolutionary hubs, and diversification of the seed plants. New Phytologist, 203, 300–309. <https://doi.org/10.1111/nph.12782>

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).