**Discussion: limitation of PEG to describe field germination**

Requirements determined with PEG solutions might not be appropriate to describe field seed germination (Camacho 2021), so direct soil water potential measurements might be needed (Bullied et al. 2012). Soil textural properties could influence the response of the seed to water potential, and this could result in different germination behaviours (Camacho 2021). Comparing osmotic and matrix potentials using PEG solutions as well as soil matrices with different soil particle sizes, Hadas (1977) determined that water potential is important for seed germination as long as soil moisture content is not limiting, but as soon as water content or water diffusivity decrease, soil physical properties influencing water supply to the seed will play a more important role. The use of PEG solutions is a practical way to determine relative differences in water use between species, genotypes, or seed lots, but it is not an adequate system to determine accurate germination responses to water availability, which seems to be the aim of many studies. Potential for multiple species as a function of soil physical properties

Soil hydraulic conductivity thresholds identified in the present study, represent a useful parameter to be included in seed germination and seedling emergence studies, because it provides a clear limit to germination (Camacho 2021).

Camacho 2021 Aimed to compare seed germination in PEG (lab) and soil with six water potential (simulating field conditions). They found that total germination for all species significantly differed between soil and PEG under the same water potentials. Germination rate was more directly related to water potential than total germination. As a conclusion: caution must be used when considering results obtained using PEG solutions to infer germination behaviour under field conditions. Our results suggest that Kh (soil hydraulic conductivity) is the driving force of maximum germination potential by regulating water flow towards the d, while water potential might play a more important role for the ability of the seed to absorb water that is in direct contact with the seed coat. As shown here, different soil textures have different Kh thresholds below which water flow to the seed is impeded and germination collapses. The use of K thresholds can be an important tool to describe vegetation dynamics in response to climate change including geographic distribution, seasonality and desertification.

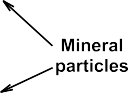
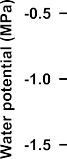
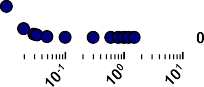
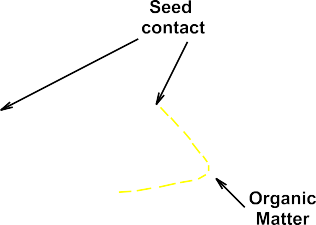
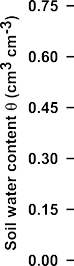
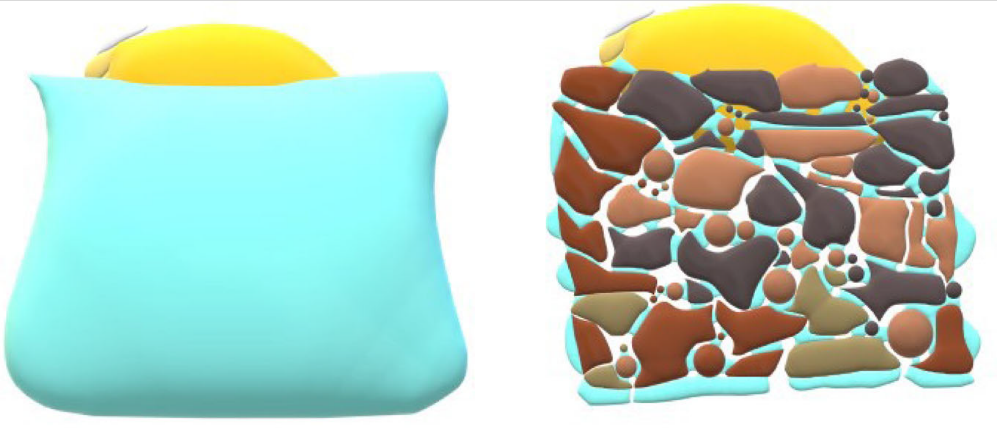


Fig 6 from Camacho 2021.

Seed collection of 1 specialist/strict alpine species, *D. langeanus*, from Mediterranean high mountain grasslands. Seed collection the 7th-8th of August 2023, from 18 different collection sites or subpopulations. Collections sites where we previously buried iButtons for 11 months (from 12/7/2021 to 29/05/2022) and we have temperatures registered every four hours. Additionally, we have hourly temperature and water potential data from 7 subpopulations (A00, B00, B07, C00, C18, D00, D12).

Seeds response to water stress depends on yearly climatic conditions, fernandez-Pascual 2014 found higher dormancy in colder years, can it translate into responses to water stress too? Or climate during seed formation and maduration?

Phenotypic plasticity in seed germination relates differentially to

overwintering and flowering temperatures

Eduardo Ferna´ndez-Pascual1\* and Borja Jime´nez-Alfaro

Results/conclusions: Temperatures during overwintering and flowering have differential effects on this plasticity (Centaurum somedanum, plasticity to degree of dormancy and sensitivity to dormancy breaking factors), allowing the plant to detect the gradient of seasonality, a main ecological feature of its distribution.

Intro: Phenotypic plasticity will be a major player in plant responses to climate change (Nicotra et al., 2010; Reed et al., 2011). Global warming (IPCC, 2013) can potentially disrupt the many interactions between climatic patterns and biological processes, such as the thermal control of seed germination (Probert, 2000). In seasonal climates, the timing of seed germination is closely linked to annual climatic cycles to ensure that seedling establishment occurs in the favourable season

(Donohue et al., 2010), but there is a risk that this relationship will be disrupted by climate warming (Walck et al., 2011). In a changing climate this phenotypic plasticity becomes of the utmost importance, as it may be the key for quick plant responses to new conditions (Matesanz

et al., 2010; Walck et al., 2011).

Nonetheless, predicting germination responses to climate change is a challenge for plant ecologists. (F-P 2014)

Info about germiantion hidrotimes Differences in hidrotimes can be result of ????

In the long term, local hidrotimes differences can select genetically based differences in xxxx though clinal variation and local adaptation (Wagmann et al.,2012; Fernandez-Pascual et al., 2013)

A local dormancy cline is related to the seed maturation environment, population genetic composition and climate

Seed dormancy varies within species in response to climate, both in the long term (through

ecotypes or clines) and in the short term (through the influence of the seed maturation environment). Something like that but about base water potential!!

Upon dispersal, these seeds show primary dormancy, either total (i.e. no germination under

any conditions) or conditional (i.e. germination under a restricted set of conditions) (Baskin and Baskin, 1998; Fenner and Thompson, 2005). In some cases, the seeds that do not meet adequate germination conditions enter secondary dormancy as a response to further environmental cues (Brandel, 2005; Kepczynski et al., 2006; Leymarie et al., 2008). These dormancy cycles (Batlla and Benech-Arnold, 2007) go on throughout the year, matching the annual temperature cycles, and have been termed the dormancy continuum (Baskin and Baskin,1985).

At any given time, spatial variation in seed dormancy can be observed among individuals and populations of the same species, as a consequence of different stages in the dormancy continuum.

Long-term effects arise from sustained climatic differences among sites, which may result in inheritable dormancy differences through ecotypes (Hufford and Mazer, 2003) and clinal variation (Montague et al., 2007). Short-term effects are produced by the specific weather during the seed maturation season, and are usually termed the parental or maternal environment effect (Fenner,

1991; Donohue, 2009. This issue is partially addressed by common garden experiments, where seeds with controlled genetic origin are matured under controlled conditions. Such an approach has confirmed that low temperatures and water availability during seed maturation result in more dormant seeds (Wright et al., 1999; Allen and Meyer, 2002; Luzuriaga et al., 2006; Qaderi et al., 2006; Hoyle et al., 2008; Figueroa et al., 2010). DISCUSSION

Most experiments on seed maturation under controlled conditions actually reported a positive

correlation between water availability and dormancy (Allen and Meyer, 2002; Hoyle et al., 2008).

Fixed local adaptation is expected when the environmental variation is at a greater spatial scale than gene flow, while the opposite situation would favour plasticity through parental environment effects (Galloway, 2005).

**Seeds of future past: climate change and the**

**thermal memory of plant reproductive traits**

Eduardo Fern´andez-Pascual1,2,∗ , Efisio Mattana3 and Hugh W. Pritchard1

Web of knowledge search for hidrotime models!!! Hydro memory??

Importantly, while seed reproduction responds to its instantaneous thermal environment, there is

also evidence of phenotypic plasticity in response to the thermal history experienced by the plant’s recent ancestors, by the reproducing plant since seedling establishment, and by its seeds both before and after their release. This phenotypic plasticity enables a **thermal memory** of plant reproduction, which allows individuals to acclimatise to their surroundings. The effects of a warming environment on plant reproduction cannot be reduced to a qualitative interpretation of absolute positives and negatives. Rather,

these effects need to be understood in terms of changing rates and thresholds for the physiological process that underlie reproduction by seed.

INTRO:

In a climate change context, the ability of a plant species to persist in its current habitat or to migrate to new sites will depend on successful reproduction by seed. Seed traits affect all levels of plant ecology from population dynamics (Huang *et al.*, 2016) to community assembly (Larson & Funk, 2016) and species distributions (Bykova *et al.*, 2012).

As Cochrane *et al.* (2015) showed, there is ample intraspecific variability in seed traits, which can provide the raw material for acclimatisation and/or adaptation to new climates. Intraspecific variability can be the result of either genetic differences (Fern´andez-Pascual *et al.*, 2013) or phenotypic plasticity (Fenner, 1991), but the latter provides the fastest way for plants to adjust to their environment (Nicotra *et al.*, 2010).

Evidence of the effect of climate change on plant reproduction is accumulating rapidly. (F-P 2019)

Plant phenotypic plasticity in a changing climate

Glossary

**Adaptive plasticity**: Phenotypic plasticity that increases the global fitness of a genotype (Figure 2).

**Epigenetic**: Includes the mechanisms of gene regulation that lead to heritable but potentially reversible changes in gene expression without changing the DNA sequence of the gene (Box 1).

**Fitness:** The fitness of an individual is taken as the relative abundance and success of its genes (often measured as the number of surviving offspring) over multiple generations. In many cases, especially with large or long-lived species, direct estimates of fitness are not feasible and total biomass, seed number or biomass, survivorship or growth rates of a single generation are used as proxies.

**Genome plasticity**: A change in genome structure or organization associated with environmental signals. leading to the evolution of new phenotypes might result from mutational hotspots, genome expansion transposable elements or somatic recombination.

**Genotype**: When we refer to a genotype we do so in a population genetic sense not in reference to a molecular sequence of a single gene but to the complete genome.

**Phenotype**: The appearance or characteristics of an organism resulting from both genetic and environmental influences. In our terms, all organisms have a phenotype not just those expressing a mutation in a given gene of interest.

**Phenotypic plasticity**: The range of phenotypes a single genotype can express as a function of its environment.

**Plant functional traits**: Quantitative traits related to the fitness and success of individuals in a given environment, they provide good indicators about species' ecologies (e.g. what growth rates they are likely to exhibit. What recruitment strategy they rely on) and are often related to competitive status, commonness/rarity or dominance in the community (Box 2).

**Plant functional types**: Categorical assessments enabling plant species to be grouped according to functional position in a community or ecosystem. For example, classifications can be based on growth form (e.g. herb, grass. shrub). nitrogen fixing status. photosynthetic pathway or leaf longevity.

Plant species can adjust to these novel conditions through phenotypic plasticity (see Glossary), adapt through natural selection or migrate to follow conditions to which they are adapted; these options are not mutually exclusive.

Plasticity, therefore, can both provide a buffer against rapid climate changes and assist rapid adaption [2,9]. Thus, we argue that, in the context of rapid climate change, phenotypic plasticity can be a crucial determinant of plant responses, both short- and long-term.

Plasticity is a characteristic of a given trait in response to a given environmental stimulus, rather than a characteristic of an organism as a whole. Likewise, some responses are examples of adaptive plasticity, providing a fitness benefit, whereas others are inevitable responses to physical processes or resource limitations [18,19]

The consensus from the theoretical literature is that adaptive phenotypic plasticity should evolve in

heterogeneous environments where signals of environmental conditions are reliable [19,20]

Plasticity in seed traits has also been documented in several species. For example, both warmer developmental temperatures [40,41] and maternal drought stress [42] can decrease seed dormancy. Dormancy prevents germination when the environment is unlikely to sustain subsequent plant growth; thus, seeds with reduced dormancy status might be more likely to germinate in inappropriate conditions. Seed longevity can also be plastic; for example, changes in temperature and rainfall experienced during seed development have the potential to halve seed longevity [44].

For example, breeding for plasticity in water use traits could lead to better survival and higher average yields [68]

**Interacting Effects of Phenotypic Plasticity and Evolution on Population Persistence in a Changing Climate**

Coupled ecological and evolutionary changes are therefore expected under climate change (Reed 2011).

Regional populations, however, are often locally adapted to a more limited range of conditions (e.g.,

temperatures) than that experienced by the species as a whole (Reed 2011).

Two phenomena can facilitate adaptive tracking of temporal changes in the environment: adaptive evolution (changes in population gene frequencies across generations that result in phenotypes that are more likely to persist in new environments) and adaptive phenotypic plasticity (fitness-enhancing responses by individuals to environmental cues) (Reed 2011).

For evolution to occur, at least some of the variation among individuals in traits affecting survival and reproductive success must be transmitted from parents to offspring (Reed 2011).

Longer summers and shorter winters might also lead to prolonged droughts in some regions, which would select for phenological changes in plants.(Reed 2011)

Adaptive plasticity in key traits may allow populations to track shifting selection pressures without much evolution (Reed 2011).

The persistence of populations and species in the face of environmental change is ultimately shaped by dynamic and often complex feedbacks between ecology and evolution (Kinnison & Hairston 2007).

Ecological factors include direct and indirect effects on births, deaths, dispersal rates, and species interactions, whereas evolutionary factors include changes in the genetic and phenotypic constitution of populations (Parmesan 2006).

Typically, ecological and evolutionary responses to environmental change are considered separately (Ferri`ere et al. 2004; Kokko & Lopez-Sepulcre 2007; Pelletier et al. 2009). Evolution, however, often occurs rapidly and can influence contemporaneous ecological dynamics (Hairston et al. 2005). Global climate change will not only affect migration patterns, biotic interactions, and local population dynamics, but also the selective pressures experienced by populations.

If the mean phenotype does not correspond to an adaptive peak (i.e., if local adaptation is imperfect), mean absolute fitness is reduced relative to the optimum, and the population experiences directional selection uphill

toward the nearest peak (Lande 1976). Deviation of the mean phenotype from the optimum is called the lag, whereas the relative decrease in mean fitness resulting from the lag is called the lag load, or evolutionary load (Lynch & Lande 1993; B¨urger & Krall 2004).

Local climates might become more variable and extreme weather events more frequent (Easterling et al. 2000), in which case populations experience selection that fluctuates more in sign and magnitude. The latter is expected to favor increased plasticity, although several factors might limit evolutionary changes to phenotypic plasticity.

Phenotypic plasticity, the environment-dependent expression of phenotypes by genotypes, can substantially alter the phenotypic distribution (mean and variance) of populations over time without a genetic change. Plasticity is evolutionarily favored when the environment is heterogeneous in time or space, selection favors different phenotypes in different environments, no one phenotype has greatest fitness across all environments, and reliable cues allow organisms to respond effectively (Bradshaw 1965; Via & Lande 1985; Gomulkiewicz & Kirkpatrick 1992; Scheiner 1993).

Plastic and evolutionary responses to the resulting artificial selection can be determined statistically with reciprocal-transplant experiments (e.g., Potvin & Tousignant 1996)

Nevertheless, if plasticity entails substantial energetic costs that reduce fitness, selection is expected to favor generalist (high plasticity) strategies only when ecological dynamics are highly variable or cyclic. Otherwise, selection should favor low-cost specialist (low plasticity) strategies (Svanb¨ack et al. 2009).

The seed germination spectrum of 528 plant species: a global meta-regression in relation to temperature and water potential

Keyvan Maleki1, Elias Soltani2, Charlotte E. Seal3, Hugh W. Pritchard4, Jay Ram Lamichhane5

INTRO: Water potential is the most important factor required for successful seed germination, influencing the vigour and final germination level/percentage. The soil is the main source of water for seeds from the environment (Bewley et al., 2012; Zhang et al., 2020).

This concept of the thermal parameters of germination can be expanded by incorporating different water potentials, leading to hydrotime and hydrothermal time models describing the seed response above a base water potential for germination (Kb)and its interaction with temperature, respectively (Gummerson, 1986; Dahal & Bradford, 1994; Finch-Savage et al., 2005; Donohue et al., 2010; Bewley et al., 2012)

The concept of ecological niche has been used to define the breadth of thermal and moisture ranges in which seeds should be able to germinate under current or future climatic conditions (Porceddu et al., 2013; Sultan, 2015; Catelotti et al., 2020; Ordonez-Salanueva et al., 2021). While the thermal time approach has been used to predict the consequences of climate change (Orru et al., 2012; Seal et al., 2017; Dantas et al., 2020), hydro time and hydrothermal time quantification should better enable predictions of the impact of global environmental change on species’ emergence and habitat patterns.

RESULTS: Instraspecific variation **Base water potential (b) for wild species = 0.448 MPa.** b values showed the lowest variation among the plant categories

Overall, Ψb values differed considerably among plant species, ranging from a lowest value of -6 MPa for Atriplex halimus (a non-tropical tree species) to nearly -0.2 MPa observed for Stipa grandis (a forage and rangeland species). Range Ψb of wild species (from -2.62 for Pectocarya heterocarpa to -0.34 MPa for Erodium cicutarium).

Lampei et al., 2017

DISCUSSION:

Although we did not focus on habitat-specific strategies, our results highlight the need for future research on the environmental and abiotic conditions (i.e., environmental and physico-chemical) which may limit the emergence of plant species (Tudela-Isanta et al., 2018).

They found less literature on Ψb, Nonetheless, studies published in the last decade have focused more on seed Ψb compared with those published before 2011. Undoubtedly, with concerns growing about the wider impacts of climate change on drought, a wider dataset on species’ germination responses to water potential would be valuable. calls for further research as germination response to water availability is one of the most important environmental driver for adaptation of plant species.

**Will among-population variation in seed traits improve the chance of species persistence under climate change?**

Anne Cochrane1,2\*, Colin J. Yates2, Gemma L. Hoyle1 and Adrienne B. Nicotra1

**Results** The evaluated studies provide compelling evidence that among population variation in traits underpinning seedling emergence, growth and establishment is widespread. Contrary to expectations, environmental gradients do not appear to be reliable predictors of variation among populations and responses are often individualistic

**Main conclusions** If we ignore among-population variation in seed traits, or assume it will follow simple environmental clines, we do so at our own peril. The consequences of such an approach are likely to include biased forecasts of future range dynamics, hindering identification of the genetic material most appropriate for conservation, restoration and management. Further research that integrates ecology and emerging evolutionary genetic techniques to identify the distribution of seed traits within foundation species and the mechanisms driving them is urgently required to guide the management and maintenance of systems in the face of rapidly changing climates.

INTRODUCTION

Changing climatic conditions are expected to affect a range of plant life-history phases, including phenology; however, this impact will potentially be most severe on the early developmental stages in a plant’s life cycle (Hedhly *et al*., 2009; Walck *et al*., 2011). Seed mass influences seedling survival (Moles & Westoby, 2004a; Metz *et al*., 2010), seed dispersal is a mechanism for dealing with environmental variability and uncertainty (Venable & Brown, 1988), seed dormancy spreads the risk of temporal variance in germination success over multiple seasons (Venable & Brown, 1988) and germination timing influences the number of seeds that become seedlings and their subsequent survival (Simons, 2009). These key traits will play important roles in determining the ability of species to shift ranges or recover from disturbance and can be linked to local or global extinction probabilities (Fenner & Thompson, 2005; Walck *et al*., 2011).

It is well established that flowering phenology can show clear geographic differentiation across a wide range of species, generally correlated with climate at latitude or elevation (Rathcke & Lacey, 1985). Similarly, among-population variation in leaf traits is important in describing plant performance under different environmental conditions (Messier *et al*., 2010). As the climate changes, populations along environmental gradients will be disproportionally affected, with threats to different habitats and species expressed in different ways. Understanding the pattern of variation in vulnerability among populations and between developmental stages is critical for accurately predicting the impacts of climate change on species (Dawson *et al*., 2011).

Ooi *et al*., 2012

The interaction between plant and environment begins with seed germination, the first major life-history transition, often a serious population bottleneck and one of the most dramatic events in a plant’s life cycle (Donohue *et al*., 2010). Germination timing is especially important: in fireprone Mediterranean-climate ecosystems timing germination to coincide with winter enables adequate seedling growth prior to the onset of summer drought (Moles &Westoby, 2004b), as later season drought stress is a common cause of seedling mortality. Physiological dormancy is the ability of seeds to postpone germination despite optimal environmental conditions, a trait that is particularly important in unpredictable and unreliable environments. (Cochrane 2014) Rapid environmental change is expected to affect seed strategies and lead to significant changes in seed responses (Cochrane 2014 este artículo de among-population)

We know that soil water potential can modify the temperatures over which germination occurs, and vice versa, affecting both rate and percentage of germination (Alvarado & Bradford, 2002). Soil warming in a temperate grassland altered recruitment of perennial species as a result of changes in soil water potential (Hovenden *et al*., 2008). germination-triggered rainfall events rather than temperature *per se* (Kimball *et al*., 2010).

Among-population variation in seed traits is thus predicted to increase with increasing range size and heterogeneity. We suggest that among-population variation in seed traits corresponds to a combination of environmentally induced and genetically fixed differences among populations of a species and may be a sign of local adaptation or genetic drift leading to differentiation in trait means and plasticities across populations. (Cochrane 2014)

The spatial variation we see in morphological and physiological traits *in situ* may reflect genetic differentiation (Linhart & Grant, 1996), including adaptation to local climate (Davis *et al*., 2005), but may also reflect environmentally induced phenotypic plasticity (Nicotra *et al*., 2010). Genetic differentiation across a

species’ range reflects a combination of random processes (e.g. drift) and selective processes (e.g. evolution), leading to ecotypic differentiation which may confer local adaptation. Early life stages are likely to be the first to be exposed to new environments, and as such are anticipated to exhibit local adaptation (Donohue *et al*., 2010). Although it is often difficult to separate trait variation from environmental variation, much of the variation among plant populations appears to reflect direct effects of the environment (i.e. phenotypic plasticity; Ackerly *et al*., 2000).

To test origin of variation (genetic vs plasticity) need of reciprocal transplant or common garden experiments (e.g. Etterson, 2004). Studies of species introductions beyond their natural distribution have provided some convincing evidence that local adaption to novel conditions can occur in seed traits (Kudoh *et al*., 2007), but can also be facilitated by phenotypic plasticity (Zhao *et al*., 2013).

Another concern is that plasticity may lead to a mismatch between environmental cue and germination response. Instead of responses increasing resilience (e.g. diversified strategies that aim to avoid risk), seeds may become ‘less discerning’ about when and where they germinate (Hoyle *et al*., 2008b), and plastic responses to the novel environment may reduce fitness.

The available studies provide evidence that among-population variation exists, and that variation is often associated with climatic gradients. There are simply too few studies that explain within-species variability in seed traits or show what leads to these differences.

Other more specific references to hydrotime

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