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The impact of transgenerational plasticity on seed germination
Vliv transgenerační plasticity na klíčení semen

Bachelor's thesis

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Poděkování

Moc děkuji prof. RNDr. Zuzaně Münzbergové, Ph.D. za odborné vedení, cenné rady, ochotu a přívětivý přístup při zpracovávání mé bakalářské práce, díky kterým mohla vzniknout. Hodně mě to naučilo. Děkuji také svému okolí za podporu ve všech formách.



Čestné prohlášení

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

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Abstrakt

Klíčení semen je zásadním procesem v životním cyklu rostlin. Je ovlivněno nejen aktuálním prostředím semene, ale také podmínkami prostředí rodičů semene díky jevu zvanému transgenerační plasticita. Transgenerační plasticita funguje prostřednictvím dvou skupin mechanismů – epigenetických modifikací a modifikací semene. Ty umožňují rodičovským rostlinám vyvolat u svých potomků reakci na podmínky, které zažily. Účinky transgenerační plasticity se liší u jednotlivých druhů, a dokonce i kultivarů a jsou buď pasivní, nebo aktivní reakcí. Aktivní reakce mohou zvýšit šance daných jedinců na úspěch, protože rostlina je schopna přizpůsobit se měnícím se podmínkám. Pasivní reakce, které nejsou vzácné, mohou být známkou toho, že měnící se podmínky mohou rostlinu ohrozit. Transgenerační plasticita ovlivňuje různé aspekty klíčení, od životaschopnosti a životnosti semen přes dormanci až po procento vyklíčených semen nebo dobu klíčení. Zastínění v rodičovském prostředí významně ovlivňuje všechny tyto aspekty a často vyvolává aktivní reakci. Nízká dostupnost vody má znatelný negativní vliv na procento klíčivosti. Míra dostupnosti dusíku vykazuje u jednotlivých druhů kontrastní výsledky. Výzkum transgenerační plasticity má mezery, které lze dále studovat. Málo prozkoumanými oblastmi jsou (1) vliv koncentrace CO₂ v atmosféře a (2) symbionti přenášení z mateřských rostlin na semena jako mechanismus transgenerační plasticity. Ve světě, kde dochází k rychlým změnám klimatu, jsou znalosti o tom, jak rodičovské prostředí ovlivňuje další generace, důležité jak pro ochranu přírody, tak pro přímé využití člověkem, například v zemědělství.

Klíčová slova: transgenerační plasticita, klíčení, mateřské vlivy, klimatická změna

Abstract

Seed germination is an essential process in the life cycle of plants. It is influenced not only by the seed's current environment, but also the environmental conditions of the seed's parents thanks to a phenomenon called transgenerational plasticity. Transgenerational plasticity functions through two groups of mechanisms – epigenetic modifications and modifications of the seed. These enable the parental plants to induce response to the conditions, they experienced, in their progeny. The effects of transgenerational plasticity differs among species and even cultivars and is either a passive or active response. Active responses may increase the chances of affected individuals to succeed, meaning the plant is able to adapt to changing conditions. Passive responses, not rare, can be a sign that changing conditions might threaten the plant. Transgenerational plasticity affects various aspects of germination, ranging from seed viability and longevity, through dormancy to percentage of germinated seeds or time of germination. Shading in parental environment significantly influences all the aspects, often causing active response. Water stress has notable negative effect on germination percentages. Nitrogen availability is showing contrasting results among species. Visibly little studied areas are (1) the effects of concentration of CO₂ in atmosphere and (2) the symbionts transferred from maternal plants to seeds as a mechanism of transgenerational plasticity. Research of transgenerational plasticity has gaps that can be studied further. In a world undergoing rapid climate change, knowledge of how parental environment affects the next generations is important both for preservation of nature and for direct human use, e.g. in agriculture.

Key words: transgenerational plasticity, germination, maternal effects, climate change

Contents

1. Introduction.....	1
2. Definition.....	2
3. Mechanisms	3
3.1 Epigenetic modifications.....	3
3.2 Modifications of the seed.....	4
3.2.1 Seed provisioning – nutrients	5
3.2.2 Seed provisioning – amount and composition of other stored compounds.....	8
3.2.3 Morphologic modifications	12
4. Influence of TGP on germination	14
4.1 Seed viability and longevity	14
4.1.1 Seed viability	14
4.1.2 Seed longevity	14
4.2 Seed dormancy	16
4.2.1 Exogenous versus endogenous dormancy	16
4.2.2 Primary versus secondary dormancy	17
4.3 Germination percentage	18
4.3.1 Light environment	19
4.3.2 Water stress	20
4.3.3 Heavy metals	20
4.3.4 Nitrogen.....	21
4.3.5 Temperature	22
4.3.6 CO ₂	22
4.4 Germination time	22
5. Conclusions.....	26
6. Bibliography.....	29

1. Introduction

Germination is critical for the successful reproduction of plants, a key part in their life cycle (Penfield, 2017). The plants need the seeds to survive until the time is right for germination. Then they need the seeds to overcome dormancy, germinate in high percentages and fast enough, so the emerged seedlings are able to gain enough space and resources among competition (Violle *et al.*, 2009). To accomplish this, the seeds need adequate conditions, such as certain temperature, moisture, light conditions, or soil quality (Fenner, 1985; Baskin and Baskin, 2014).

Where and when the seed germinates also partly determines the conditions for the emerging seedlings. Therefore, it is desirable for the parental plants to be able to prepare the seed for the conditions they will probably germinate in (Donohue and Schmitt, 1998; Penfield, 2017). Apart from the seed's current environment, seed germination depends also on the seed's genotype and conditions experienced by parental plants (Roach and Wulff, 1987; Mondoni *et al.*, 2014). The latter is a phenomenon called transgenerational plasticity. Transgenerational plasticity allows parental plants to pass on information about their external environment to their seeds and modify their germination performance (Kempthorne, 1969; Wolf and Wade, 2009). The response of seed germination to the effects of transgenerational plasticity can be either passive or active (Violle *et al.*, 2009). In the case of passive response, the success of progeny depends on whether the parental plant experienced suitable conditions or not. If it did, the seed quality will be higher, and the progeny will do well. If parental plant experienced some kind of distress, the seed quality will be lower and progeny will do worse than in the first case (Sultan, 1996). Active answer, on the other hand, allows progeny to actively respond to parental conditions. Even in cases when parental plants grew in unsuitable conditions, seed quality can be high and their progeny is able to perform well or even better than seeds from plants experiencing good conditions (Violle *et al.*, 2009).

Whether a plant is able to respond actively may influence wellbeing of the individual, population or possibly whole species (Mondoni *et al.*, 2014). In the currently rapidly changing environmental conditions, it is important to understand how plants are affected by the changes. Knowledge of which plants are able to adapt to the changes of climate and how is becoming increasingly important for species protection, controlling the spread of invasive species or human use in agriculture (Dyer *et al.*, 2010; Baskin and Baskin, 2014).

The goal of this thesis is to summarize information on the influence of transgenerational plasticity on germination. In its first part, the thesis summarizes the mechanisms through which transgenerational plasticity functions, describes them, sorts them into groups and gives examples of studies where individual mechanisms appear as explanations of observed effects.

The second part describes the influence of transgenerational plasticity on different aspects of germination using examples of studies describing the effects of various stresses (temperature, water stress, nutrient deficiency or overfertilizing and more).

2. Definition

Transgenerational plasticity (TGP) accompanied by transgenerational effects (TGE) represent a phenomenon when phenotype of progeny is formed not only by its genotype and current environment, but also by the environment and phenotype of the parent (Kempthorne, 1969). TGP allows the progeny to actively respond to the stresses the parent experienced and improve their response. It helps progeny experiencing parental environment induce the response faster than individuals in non-parental environment which enhances fitness of the former (Agrawal, Laforsch and Tollrian, 1999; Galloway, 2005; Donohue, 2009; Li *et al.*, 2018). Transgenerational plasticity and effects usually depend on the maternal plant as the seeds mature under its direct influence (Galloway, 2005). Therefore, TGP traditionally used to be referred to as maternal effects. However, in outcrossing species, paternal plants might play an important role in transferring transgenerational effects as well (Roach and Wulff, 1987) and in many species it is not possible to distinguish the maternal effects from paternal as they are entirely clonally reproducing or selfing (Dyer *et al.*, 2010; Rendina González *et al.*, 2018). Hence, transgenerational plasticity is a more concise term because it permits more inclusive and precise definition (Agrawal, Laforsch and Tollrian, 1999; Dyer *et al.*, 2010).

Specific definition of TGP has changed over time. According to Roach and Wulff (1987) TGP includes three classes – cytoplasmic genetic, endosperm nuclear and maternal phenotypic. According to Donohue (2009), in broader definition, it involves the effects of cytoplasmic inheritance (i.e. maternal inheritance of plastids), endosperm and seed coat which are mostly or wholly of maternal origin, maternal provisioning of the seed and the influence via dispersal of seeds or phenology. On the other hand, Wolf and Wade (2009) define maternal effects as the "*causal influence of the maternal genotype or phenotype on the offspring phenotype*". They state that the term cannot be used for some phenomena for which it usually is used, e.g. genomic imprinting or cytoplasmic inheritance, because then it would be too comprehensive for use.

This section has demonstrated that TGP is defined differently by different authors. Nonetheless, general consensus is that TGP is transferred by several main mechanisms described e.g. in Latzel (2015) or Herman and Sultan (2011). Herman and Sultan (2011) sort the mechanisms into (1) seed provisioning, (2) content of proteins, hormones, and mRNAs and (3) DNA methylation and histone modification. These three categories could still be, if more generalized, fitted into Latzel's categorization. Latzel (2015) sorts mechanisms of TGP into two

groups – (1) epigenetic modifications and (2) modifications of the seeds. That seems to be the most recent and neat categorization and this work will follow it as well.

3. Mechanisms

Having defined the categories of mechanisms transferring TGP, let us now take a look at them in greater detail. Chapters below review literature on epigenetic modifications and modifications of the seed (seed provisioning, amount and composition of other stored resources, and morphologic modifications) and discuss their effects on germination.

3.1 Epigenetic modifications

The phenotypes of cells and subsequently whole organisms may differ even though their DNA sequences show no difference, nor does differ their current environment. Such effects can be caused by epigenetics, namely cellular epigenetic inheritance, when said variances in phenotypes are transmitted to progeny (Jablonka and Raz, 2009). Multiple mechanisms mediate the process and those are nucleosome occupancy and remodelling, RNA interference, relative abundance of histone PTMs (post translational modifications) and cytosine (DNA) methylation (Mozgova *et al.*, 2019).

TGE caused by epigenetic marks are dynamic. They influence individuals through their whole life and can persist through multiple generations (Latzel, 2015; Rendina González *et al.*, 2018) or also wash out completely or partially over time (Burggren, 2015). Burggren (2015) also supports the suggestion of Jablonka and Raz (2009) that *"the inheritance of some epigenetic memory traces may lead to epigenetic recall"* when in order to induce the effect again, the stressor needs to be introduced anew. Epigenetic marks are also often reset during meiosis (Tricker, 2015), because of which they might play a more important role in clonal plants where they allow clonal plasticity to interact with conventional TGE (Latzel and Klimešová, 2010).

The mechanisms of epigenetics depend on other factors than just the maternal environment. They may be genotype specific (Suter and Widmer, 2013; Münzbergová and Hadincová, 2017; Rendina González *et al.*, 2018) or interact with the environment of progeny, provide beneficial TGE, but at the same time present constraints. For instance, in *Boechera stricta* Alsdurf, Anderson and Siemens (2016) found a trade-off between drought tolerance and herbivory defense caused by DNA methylation. Guarino *et al.* (2024) discovered epigenetic changes leading to active germination response of *Arabidopsis thaliana* plants (Figure 1). Specifically, they found cytosine methylation on several major genes that may have led to higher resilience to Cr stress. In contrast to seeds from not stressed parents whose germination rates reduced under Cr stress, seeds from stressed parents showed similar germination rates even under high concentrations of Cr (Figure 1).

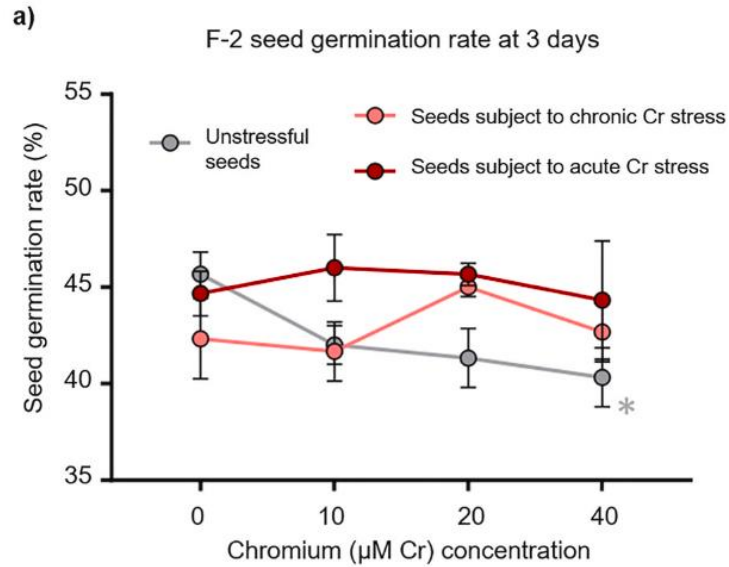


Figure 1. Seed germination rate of *A. thaliana* seeds from parents treated by different chromium (Cr) stress plus control. Under chronic Cr stress, parental plants were treated by 2.5 μM for the whole time of cultivation, acute stress means plants were treated with 5 μM for the first three weeks and then returned to non-stressful conditions (Guarino *et al.*, 2024). Seeds were treated by different amounts of Cr, data collected 3 days after sowing (figure taken from Guarino *et al.*, 2024, modified).

The literature (more reviewed e.g. in Richards *et al.*, 2017) confirms epigenetics' dependence on the environment and its part in TGP. Epigenetics can mediate resilience to various stresses may it be drought, heavy metals or high temperatures and epigenetic changes can lead to active response in the form of improved germination (Alsdurf, Anderson and Siemens, 2016; Liu, Able and Able, 2020; Guarino *et al.*, 2024). It is, though, not the only one mechanism able to do that. Let us now move on to the second large group of mechanisms – modifications of the seed.

3.2 Modifications of the seed

As for modifications of the seed, there are two important ways in which the mother plant can influence the seed. It is the amount and composition of stored resources and changes in the characteristics of the tissues surrounding the embryo (cotyledon, endosperm, seed coats) (Sultan, 1996; Lacey, Smith and Case, 1997). All these factors are known to further impact germination (Rajjou *et al.*, 2004; Donohue, 2009; but see Pers-Kamczyc and Suszka, 2022) or performance of the seedling (Mašková and Herben, 2018).

3.2.1 Seed provisioning – nutrients

Seed provisioning is the amount of resources the mother plant provides to the seeds it produces. This includes carbohydrates, proteins, lipids, minerals (e.g. nitrogen, phosphorus), (Rajjou *et al.*, 2004; Bonduriansky and Day, 2009; Mašková and Herben, 2018). Nutrients stored in the seed (nonstructural carbon, nitrogen, and phosphorus) are crucial for the germination and initial growth (Lamont and Groom, 2013). Unlike external resources, they are predictable and always available to the seedling to give it a head start, so it can grow roots and leaves faster than its competitors and have more space to obtain resources on its own (Moles and Westoby, 2006; Mašková and Herben, 2018). It is, therefore, desired by the plant to provision its offspring the best it can.

However, resources are usually limited due to small pool of nutrients in the soil (Zas, Cendán and Sampedro, 2013) or competition (Violle *et al.*, 2009; Adeyemi *et al.*, 2021) and the plant must balance the expenses (Zas, Cendán and Sampedro, 2013). In this chapter, I will focus on four main questions: (1) "How do plants determine provisioning of a particular seed?", (2) "How is provisioning correlated with seed size and mass?", (3) "How is the size and mass of a seed determined?" and (4) "How does seed provisioning and size impact germination?".

3.2.1.1 How do plants determine provisioning of a particular seed?

Seed provisioning varies between species (Violle *et al.*, 2009; Adeyemi *et al.*, 2021). It differs throughout the season (if the plant reproduces repeatedly) and by location on the stem (Mcginley and Charnov, 1988). Each seed belongs to some module of the plant and the microclimate of different modules can vary, especially on trees. Hence, different seeds may get different amounts of resources e.g. from photosynthesis (Mcginley and Charnov, 1988). Also, plants can either respond passively to nutrient limitation or actively (Violle *et al.*, 2009). Passive response in this case would be lowering the amount of seeds and/or their provisioning (Adeyemi *et al.*, 2021), whereas active response would be changing the provisioning in a way to improve the offspring's fitness. For example, if the plant lowered seed number, it might compensate by their provisioning or vice versa (Violle *et al.*, 2009). In other words, how well provisioned a particular seed will be, depends on the amount of resources available to the plant, but also on the microclimate of the module in which the seed is located, and response (passive or active) of the plant to the particular conditions. It is, though, usually talked about big seeds and small seeds (measured by size or mass) instead of how provisioned the seed is (Cordazzo, 2002; Pers-Kamczyc and Suszka, 2022; Razzaque, Heckman and Juenger, 2023; etc.).

3.2.1.2 How is provisioning correlated with seed size and mass?

In a synthesis, Lamont and Groom (2013) state that "*seed mass is a good index of plant investment in C*", because "*organic component of seeds is made up of units of CH₂O (and sometimes CHO for those that store fats and oils)*", but based on research data they come to the conclusion that N and P are more important for the mass (Figure 2). Lamont and Groom (2013) also declare that N and P are more important for seedling growth in the first year than C, because they are essential for binding new carbon through photosynthesis. Previous research tried to model seed mass/size dependence on provisioning multiple times. Smith and Fretwell (1974) made a one-nutrient model which is not adequate for more nutrient pools that usually exist in soil (Mcginley and Charnov, 1988). Mcginley and Charnov (1988) then followed them and made a model for two and more nutrients model on C/N ratio.

3.2.1.3 How is the size and mass of a seed determined?

The most beneficial size of a seed varies for different environments depending on what the emerging seedling needs to achieve for successful establishment. In competitive environments, smaller seeds are preferred, because they tend to germinate faster (Murali, 1997; Souza and Fagundes, 2014). A seedling that germinated faster can faster grow larger organs and outcompete others in the access to nutrients (Mašková and Herben, 2018). In competitive, therefore limiting conditions, plants also have to decide how they will invest available resources, often choosing between seed size and number (for more see section 3.2.1 *Seed provisioning*). Moles and Westoby (2006) found a negative correlation between seed mass and seed density, adding to the claim that in competitive environment, smaller seeds are favoured.

In non-competitive environments, larger seeds are more beneficial. They contain more nutrients from which they can draw and produce larger and more viable seedlings (Dyer *et al.*, 2010; Souza and Fagundes, 2014). In unpredictable or heterogenous environments, it might be the best strategy to produce seeds with greater size variation. Zas and Sampedro (2015) demonstrate that in a study on Maritime pine. Despite lower mean weight, they found a wider seed weight variation in trees growing in less favourable conditions, a possible active answer to unpredictable environment.

TGP can either support the needed seed size via active response or submit to the environmental conditions in passive response (Violle *et al.*, 2009). As an example of passive response, Wijewardana *et al.* (2019) confirmed that soil moisture has positive effect on soybean seed biomass and germination traits. With increasing water stress, seeds were smaller, fewer, more shrivelled and germination rate decreased along with its speed. Another example is Pers-Kamczyc and Suszka (2022) who studied seed size, germination capacity and offspring performance on *Taxus baccata L.* from long-term fertilized and unfertilized trees.

According to their results, seeds from fertilized tree were larger but with worsened germination capacity (medium and large seeds still germinated better than small ones). Probably a passive response was found by Murali (1997). He found, that depending on the fruiting season, tropical trees produce either larger seeds with longer germination time (rainy season) or smaller seeds with longer viability (dry season).

There are also many cases, where it is not as obvious, whether the response is active or passive. For example, under elevated maternal CO₂, *Bromus erectus* plants produced larger seeds relative to ambient CO₂. Nevertheless, these conditions also had a negative impact on seedling size (Steinger, Gall and Schmid, 2000). Or secondly, artificially shaded plants studied by Marin et al. (2019) produced larger seeds than non-shaded plants. However, no effect on germination was recorded, hinting no effect of the shading on the seeds' quality.

The effects of TGP on seed size are common – passive or active. Noticeable is that even when the effect results in larger seed size and seems positive, it does not always lead to positive traits later in its life cycle (as in seedling vigour, germination, or seed longevity).

3.2.1.4 How does seed provisioning and size impact germination?

Adeyemi et al. (2021) studied pod and seed trait variations of legumes combined with nutrient abundance and deficiency. Seed nitrogen concentration (SNC) and germination percentage were highly positively correlated which was expressed in lower germination of seeds with lower content of nitrogen. Violle et al. (2009) also found a positive correlation between SNC and germination time. As a third example, a study on three major species of Brazilian coastal dunes (Cordazzo, 2002) revealed that large seeds germinate faster and in higher percentages, probably due to the need of nutrient supply when buried under sand. More examples showing correlation between seed size and germination are mentioned in *4. Influence of TGP on germination*. It is obvious that seed's nutrient provisioning should not be overlooked as a germination impacting factor. However, there is still more to take in account and the chapter that follows moves onto considering other stored resources' role in the process.

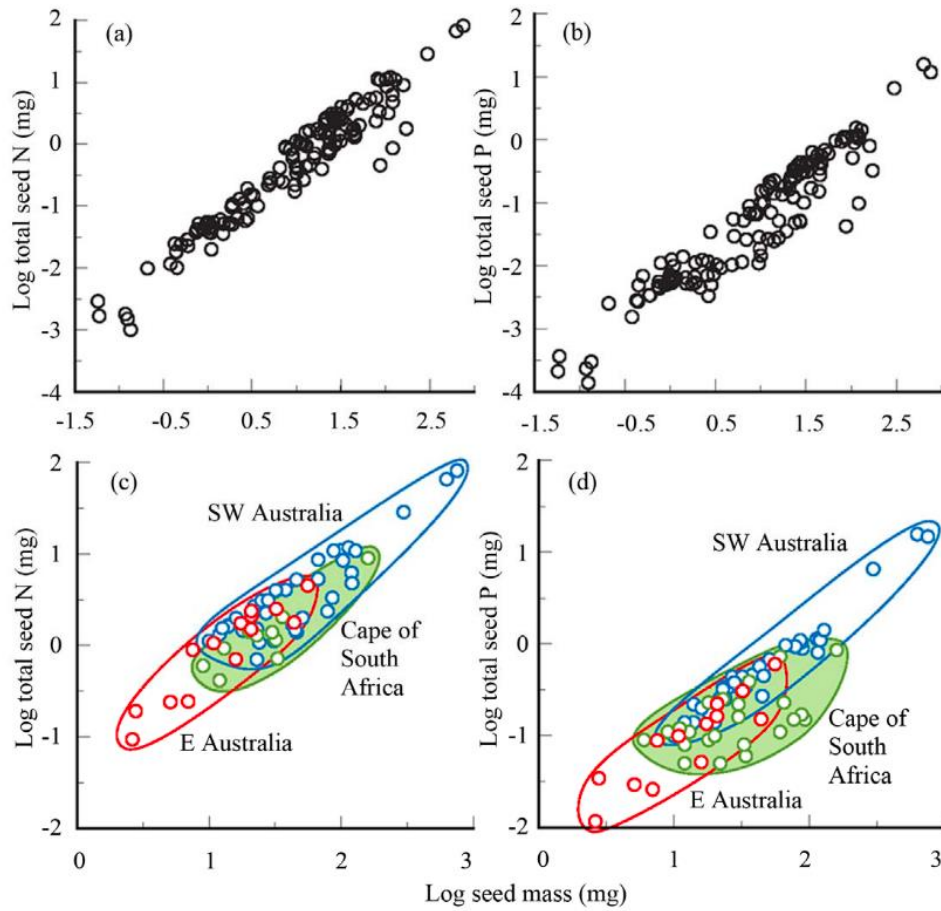


Figure 2. Relationship between seed mass and total (a) seed-N and (b) seed-P content for worldwide temperate regions (Lamont and Groom, 2013) and the equivalent (c), (d) for southwestern Australia and eastern Australia, and the Cape of South Africa for *Proteaceae* (subfamilies *Grevilleoideae* and *Proteoideae*) (figure taken from Lamont and Groom, 2013).

3.2.2 Seed provisioning – amount and composition of other stored compounds

In addition to carbon, nitrogen, and phosphorus, seed also contain many other compounds stored including (1) phytohormones, (2) RNAs and transcription factors (TFs), (3) secondary metabolites of symbionts or the symbionts themselves (Oracz and Karpiński, 2016; Gundel, Rudgers and Whitney, 2017; Mozgova *et al.*, 2019). They interact with each other. They promote or inhibit germination, dormancy, and growth, translate new proteins after germination or take a role in other important processes. The following is a brief review of these compounds of seed provisioning.

3.2.2.1 Phytohormones

Phytohormones are chemical compounds produced by plants that regulate various physiological processes (Shu *et al.*, 2016). Among others germination and seed dormancy.

They have direct effects on their own, but different signalling pathways can also interact (crosstalk) or act in synergy (Ranjan and Lewak, 1994; Oracz *et al.*, 2008). Below I list and describe several groups taking part in germination.

Two main phytohormones of seed germination and dormancy are two antagonists – abscisic acid (ABA) and gibberellins (GA) (Seo *et al.*, 2006; Lee, Lee and Seo, 2015). ABA inhibits germination (along with inhibiting biosynthesis of GA), supports dormancy and its synthesis is inhibited by light (Koornneef, Bentsink and Hilhorst, 2002; Seo *et al.*, 2006). Subsequently ABA regulates seedling and plant growth (Creelman *et al.*, 1990; Zhang *et al.*, 2017). These functions may be illustrated and reflected in ABA concentration in seeds studied by Feurtado *et al.* (2004) that decreases before germination and rapidly increases shortly after it (Figure 3).

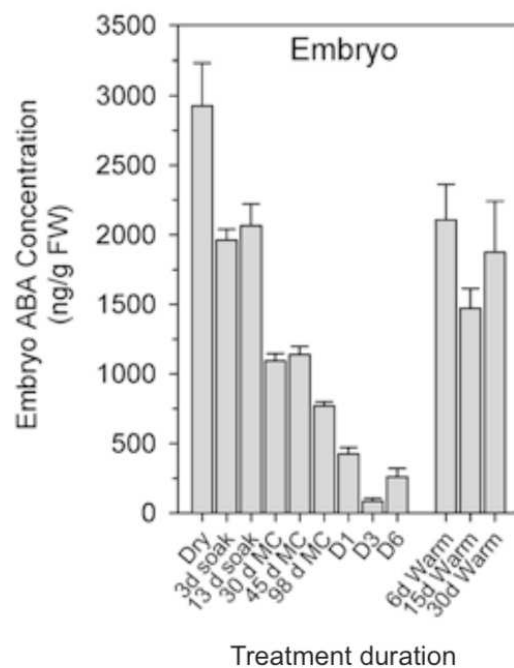


Figure 3. Embryo ABA concentration changes in western white pine seeds undergoing dormancy-breaking treatment, germination and following growth. Pre-germination decrease of ABA concentration and following increase is apparent. MC – moist chilling; D1, D3 – days after transferring seeds to germination conditions, ungerminated; D6 – days after transferring seeds to germination conditions, germinated (figure taken from Feurtado *et al.*, 2004, modified).

In contrast to ABA, GA are synthesized in the presence of light and trigger germination by inhibiting the effect of ABA (Seo *et al.*, 2006). It is done for example by activation of ABA catabolism (Gonai *et al.*, 2004). A signalling pathway of GA also leads to increase of auxin which then supports development of the embryo (Hu *et al.*, 2018).

Regulation of germination by phytohormones is complex with more variables than ABA and GA. Other phytohormones promoting germination are ethylene, cyanide, auxin, brassinosteroids or cytokinins; germination-inhibiting phytohormones include (Oracz *et al.*, 2008; Xue *et al.*, 2008; Oracz and Karpiński, 2016; Lv *et al.*, 2021; Pan *et al.*, 2023), 2016; Lv *et al.*, 2021; Pan *et al.*, 2023). During germination regulation ABA and GA both cooperate with other signaling pathways. They both regulate germination inhibition by jasmonates (JA) (reviewed in Pan *et al.*, 2023) or interact with melatonin (Lv *et al.*, 2021). GA crosstalk with e.g. auxin (Hu *et al.*, 2018), ABA crosstalks e.g. with brassinosteroids (Xue *et al.*, 2008), but many more examples could be listed as there are a number of phytohormones in the play.

Phytohormones in seeds are both provided by parental plant and synthesized *de novo*. Their content in seed depends on parental environment, but the final effect can vary among species even under the same conditions. Difference can be shown on a study by Contreras *et al.* (2009) on lettuce (*Lactuca sativa*) compared to Chen *et al.* (2020) who studied germinability after shading of the parent on soybean (*Glycine max*). Chen *et al.* (2020) found out that the seeds of shaded parents had lower ABA concentration compared to those from unshaded parents resulting in higher germinability. On the other hand, Contreras *et al.* (2009) found worse germination ability and higher ABA levels in soybean seeds from parents undergoing simulated shaded treatment, a completely opposite result.

Phytohormone levels in the seed also change throughout, before and after germination (Feurtado *et al.*, 2004; Fi(Feurtado *et al.*, 2004; Seo *et al.*, 2006; Oracz *et al.*, 2008; Li *et al.*, 2018)2006; Oracz *et al.*, 2008; Li *et al.*, 2018). During their biosynthesis, catabolism, signaling or responding to external cues phytohormones closely cooperate with genes, thus possibly being influenced by epigenetic changes, and other compounds stored in seeds (Seo *et al.*, 2006; Oracz *et al.*, 2008; Lee, Lee and Seo, 2015; Chen *et al.*, 2020; Wang *et al.*, 2021).

3.2.2.2 RNAs, regulatory proteins

Proteins (such as enzymes or transcription factors – TFs), small non-coding RNAs (miRNA, siRNA) or mRNAs participate in transcription and translation in the seed or regulation of dormancy and germination (Figure 4; Rajjou *et al.*, 2004; Donohue, 2009; Pontier *et al.*, 2012; Das *et al.*, 2015). Their amount in the seed (and therefore functioning) is inevitably tied to other me(mec(Pontier *et al.*, 2012)etic modifications (Pontier *et al.*, 2012) or regulation of phytohormone biosynthesis in the seed (Lee, Lee and Seo, 2015). They are, though, not only stored in the seed, but also synthesized *de novo* (Rajjou *et al.*, 2004; Donohue, 2009). There is a need to differentiate between the two cases as to determine whether their effects are transgenerational or not.

An example of TGP caused by RNAs is a study of Rajjou *et al.* (2004). They found that seeds germinated slower, but no less even after inhibiting translation, hinting that seeds are able to

use stored mRNAs and proteins and their content in the seed matters. A second example showing impact of RNAs stored in the seed is Liu, Able and Able (2020). Based on their results, they suggest that miRNAs play a role as a part of epigenetic mechanisms connected with transgenerational water and heat stress tolerance of durum wheat leading to better germination.

Regarding proteins as regulatory compounds, Colzi et al. (2023) studied germination of *A. thaliana* under chromium stress. They compared germination percentage under chromium stress of progeny from stressed parents to progeny of non-stressed parents. Stressed progeny germinated better than non-stressed showing active response. The authors then deduced protein-protein interaction networks finding several TFs and other proteins involved in creating the transgenerational response. Studies connecting compounds involved in transcription and translation and germination are mostly epigenetic, for more, see section 3.1. *Epigenetic modifications*.

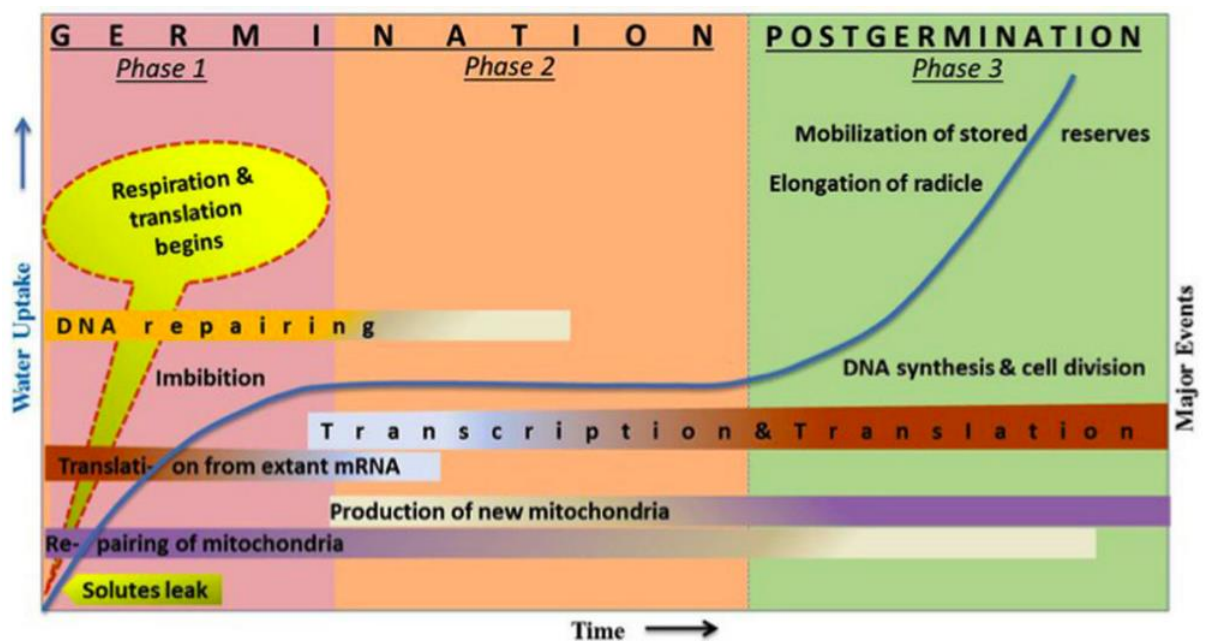


Figure 4. Germination and post-germination stages and accompanying events. *Phase 1* starts with imbibition when the dry seed uptakes water, preparing itself for respiration and synthesis of proteins and mRNAs in *Phase 2*. *Phase 2* as well as germination ends with radicle emergence through the seed coats. In the postgermination *Phase 3*, the radicle elongates and stored reserves are mobilized (Bewley, 1997). Less – more action of the major events is illustrated by colour gradients (light – dark), line graph pictures water uptake and related increase in biomass (figure taken from Das et al., 2015).

3.2.2.3 Symbionts

Plants form symbiosis with different organisms bringing them advantages in the form of higher plant resistance to herbivory or higher tolerance to drought or oxidative stress (Clay and Schardl, 2002; Kumari and Vujanovic, 2020). These symbionts or their secondary metabolites can be transmitted from the maternal plant to the seeds (Gundel *et al.*, 2021). What effects do they cause in combination with external stresses?

There are not many studies linked to symbionts, TGP and germination, nevertheless, for example Gundel *et al.* (2015) did a study on *Lolium multiflorum* seeds' longevity. When they exposed seeds of plants with and without fungal symbionts (*Epichloe* genus) to ozone, they found a contrasting response. The symbionts had a negative impact on seed longevity, even though the seed yield increased. Ueno *et al.* (2020) also found a negative effect of this symbiotic fungi on seeds of *L. multiflorum* exposed to ozone (relative to symbiont-free).

It seems that even though symbionts can bear benefits for plants, they also cause more negative effects on seeds under ozone treatment than symbiont-free plants experience. On the other hand, Kumari and Vujanovic (2020) found a positive effect of endophytic fungi and bacteria on germination of seeds coming from drought-stressed parents (compared to seeds from non-stressed parents). These examples show that symbionts can be an important factor in the seed response to parental environment, but studies on their connection to TGP are scarce and this area could be more studied.

3.2.3 Morphologic modifications

The last group of mechanisms by which the plant can transmit TGE are morphologic modifications of the seed. Endosperm and seed coat surrounding the embryo are maternal tissues, thus they directly mediate the mother's influence on the offspring (Lacey, Smith and Case, 1997). How much nutrients and other stored resources are put in these tissues may have consequences on how well the offspring performs later (Sultan, 1996; Debeaujon, Léon-Kloosterziel and Koornneef, 2000).

Morphologic modifications are responsible e.g. for faster germination of seeds with thinner pericarp in comparison with those with thicker (Sultan, 1996; Herman *et al.*, 2012). It gives them a head start in the initial phase of growth, a chance to outgrow their competition. It is often found in seeds of plants experiencing stressful conditions. To exemplify: shading, nutrient deficiency (Sultan, 1996) or drought (Herman *et al.*, 2012).

For example, Sultan (1996) did a study on light conditions, soil moisture and soil nutrients influence on *Polygonum persicaria* offspring traits distinguishing the biomass being allocated in the pericarp. She found out that seeds under light stress had thinner pericarp and germinated earlier (Figure 5), seeds under water stress were larger (with no significant change in pericarp) and had higher total germination. Seeds from plants issued by nutrient deficiency

weighed less (no change in pericarp) with no significant influence on germination. Herman et al. (2012) studied impact of drought stress on germination through two generations (grandparental, parental, and offspring). They found that TGP added up through the generations forming an active response. The result in seeds from plants experiencing drought stress in both generations was increased seed size, but lowest pericarp proportion and earlier germination (compared to all other combinations of drought and moist treatment).

Luzuriaga, Escudero and Pérez-García (2005) also researched impact of maternal environment on seed coat thickness and germination. Even though germination rate was highly influenced by the environment, all variation in seed coats was caused by maternal identity and the environment had no effect on it.

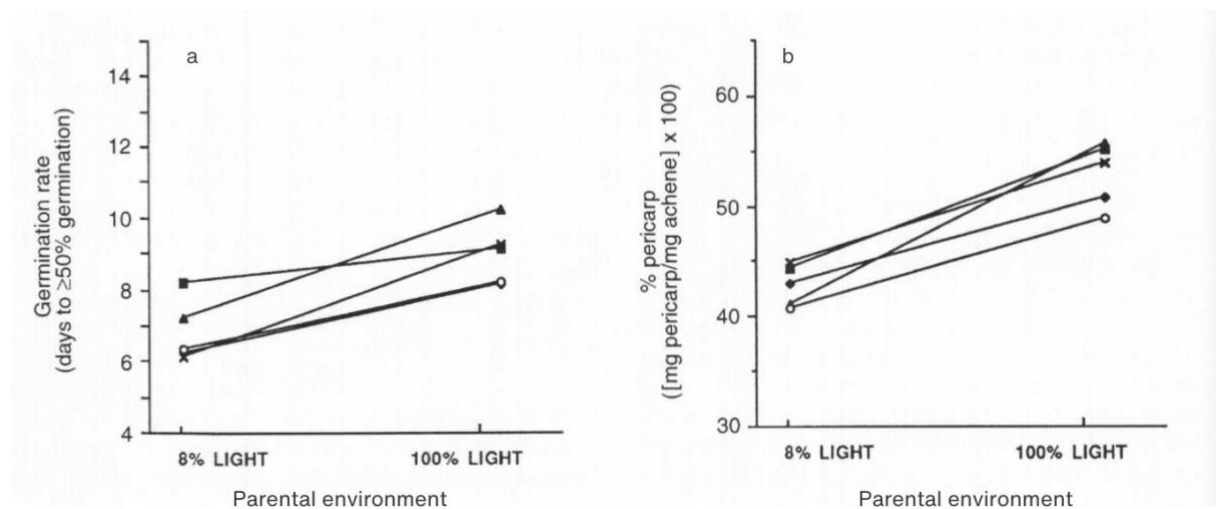


Figure 5. Reactions of five parental genotypes to low and high light, (a) germination rate, (b) pericarp proportion (figure taken from Sultan, 1996, modified).

This chapter has reviewed the mechanisms by which TGP can be mediated and presented several examples. Both epigenetic changes and modifications of the seed have an important role in the process, however studies mostly concentrate only on one of them and do not compare their influence, so whether one mechanism is dominant or how they complement each other seems to remain a question. The chapter that follows moves on to consider the influence of TGP on different aspects of germination.

4. Influence of TGP on germination

Germination starts with water absorption, i.e. imbibition (Figure 4), and ends with emergence of the radicle (Bewley, 1997; Oracz and Karpiński, 2016). It is a crucial stage and process in the plant life as it begins the life histories of a new individual (Donohue, 2009). Therefore, it is very important for the survival of that individual as well as on populational and species' level, whether the process will be successful and in what way the plant deals with external stresses. Several factors of germination can be affected (Contreras *et al.*, 2008; Herman *et al.*, 2012; Karimmojeny *et al.*, 2014). Seed longevity and viability, germination time and percentage, and percentage of dormant seeds are all important characteristics of germination with specific consequences in case of their change, whether the change is active or passive. This chapter focuses on the impact of TGP on those characteristics and the responses to parental environment it evokes, reviewing available research.

4.1 Seed viability and longevity

4.1.1 Seed viability

Seed viability is the ability of seeds to germinate under ideal conditions (Bradbeer, 1988). Viability is tested for example by tetrazolium test (da Silva Alabarce and Dillenburg, 2017). After germination test embryos of non-germinated seeds are determined viable/non-viable using colouring based on enzyme activity. Another way to test viability, used by Gundel *et al.* (2009) is a germination test conducted under ideal conditions. Determining viability is used to identify dormancy in seeds (potentially caused by external stress) in germination experiments, used for example in da Silva Alabarce and Dillenburg (2017). But, seed longevity and viability are sometimes used interchangeably (Murali, 1997; Gundel *et al.*, 2009). The parameter being studied in those cases is often longevity, therefore, let us now focus on that.

4.1.2 Seed longevity

Seed longevity is the period of time for which seeds remain viable and capable of germination (Mondoni *et al.*, 2014) and it depends mostly on temperature and moisture of the environment (Ellis and Roberts, 1980). To determine seed longevity, stored dried seeds are submitted to rapid ageing test in which they are rehydrated and then germinated in increased temperature (Newton, Hay and Probert, 2022). After, germination percentage is determined and the data are fitted in the viability equation, where v – viability; K_i – initial viability; p – days of storage; σ – the standard deviation of deaths in time (Ellis and Roberts, 1980):

$$v = K_i - (p/\sigma)$$

Seed longevity is important for the survival of species in nature. It is sometimes studied as storability (Contreras *et al.*, 2008) as it is also an important information for conservation in seed

banks and for potential reintroduction (Walters, Wheeler and Grotenhuis, 2005). Longevity differs between species and plant families genetically (*Malvaceae*, for instance, have usually higher longevity, while *Brassicaceae* lower) (Walters, Wheeler and Grotenhuis, 2005), but can also be affected by TGP, as demonstrated in the following studies.

An illustration of the dependence of longevity on parental environment temperature, is e.g. Mondoni et al. (2014). They examined longevity of *Silene vulgaris* seeds harvested from alpine (lower mean monthly temperatures) and lowland (higher mean monthly temperatures) locations and seeds of their progeny cultivated at the lowland site (Figure 6). They found that among alpine populations, seeds from plants cultivated in lowland environment had the highest longevity (also lowland populations did generally better than alpine). The authors attribute these results to genetics, but also to differential contents of mRNA caused by TGP.

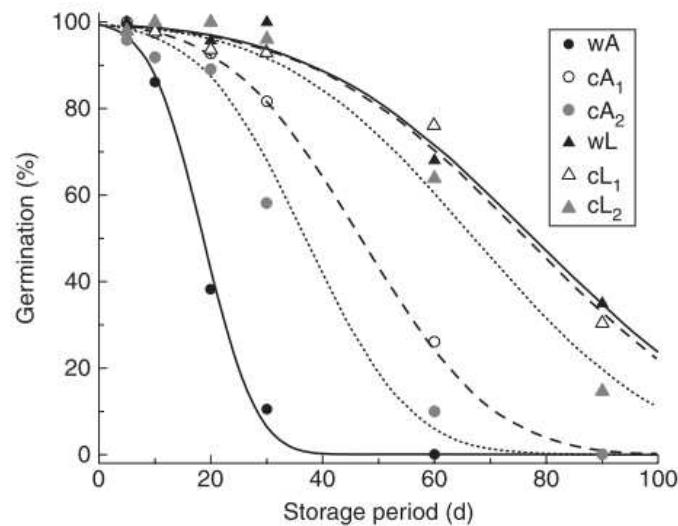


Figure 6. Survival curves (dependence of germination percentage on days of storage) of six groups of *Silene vulgaris* seeds: seeds from wild alpine and wild lowland populations (wA, wL; black symbols and full lines), seeds collected from their progeny cultivated in lowland environment in first (cA₁, cL₁; empty symbols and dashed lines) and second (cA₂, cL₂; grey symbols and dotted lines) generation (Mondoni *et al.*, 2014). Figure taken from Mondoni *et al.* (2014).

With opposite results, Kochanek *et al.* (2011) exposed two generations of *Plantago cunninghamii* parental plants to cool/warm and dry/wet conditions and measured longevity of seeds originating from them. They concluded that moisture level had only effect on seed size and temperature on seed longevity. Seeds experiencing cool conditions during maturation had higher longevity (circa 15 days), seeds from warm conditions about half as much. Similar scenario was seen in second generation, where seeds from plants moved to cool conditions

had their longevity doubled and seeds moved to warm conditions lowered. In this case, the authors suggest that the differences are caused by paternal response to environment in pollen development. Parental temperature has an influence on seed longevity, but we cannot determine universal values as outcomes vary between species as seen in the comparison of Mondoni et al. (2014) and Kochanek et al. (2011).

In addition to temperature and moisture, seed longevity also depends on parental light environment. Contreras et al. (2008) described that *Lactuca sativa* seeds matured under long days showed higher longevity than seeds matured under short days. Long day seeds were also larger than short day seeds, suggesting positive correlation between seed mass and longevity. Later, Contreras et al. (2009) found that seed longevity is higher under lower maternal R:FR ratio (in comparison with higher R:FR), corresponding to lesser shading. Mothers experiencing lower R:FR ratio also produced seeds with greater mass, implying positive correlation of seed mass and longevity.

In contrast with that implication, multiple studies focusing on correlation between seed size and longevity state that there is an inverse relation between seed weight and longevity (Thompson, Band and Hodgson, 1993; Funes *et al.*, 1999). Other studies also confirm this theory, adding that there is an important impact of external environment on longevity (Schutte, Regnier and Harrison, 2008; Satyanti *et al.*, 2018).

In conclusion, seed longevity depends on temperature, moisture and light conditions of parental environment, but also the weight of the seed, even though this relationship cannot be easily generalized. And even viable seeds sometimes do not germinate. That is the case of seed dormancy, described in the following section.

4.2 Seed dormancy

Dormancy is an important stage in the plant life cycle. In this state, seeds can overcome unfavourable conditions in which the seedlings would die otherwise, and germinate when the conditions, mostly temperature and moisture, are just right (Leadem, Landis and Thompson, 1997). Now before precisely defining the term, let us sort out the categories of dormancy.

4.2.1 Exogenous versus endogenous dormancy

Regarding the mechanism, dormancy can be sorted into exogenous and endogenous. Exogenous dormancy depends on the seed coats impermeability to oxygen or water or germination inhibitors the coat contains. Endogenous dormancy is driven by internal factors like maturity or metabolic requirements and needs moisture and a specific temperature or

after-ripening to be broken (Leadem, Landis and Thompson, 1997). TGP can possibly have effect on both (see section 3. *Mechanisms*).

4.2.2 Primary versus secondary dormancy

Two other types of dormancy are described – primary and secondary (Bewley, 1997). Secondary dormancy is caused by external factors after the seed is already dispersed (Figure 7). Primary dormancy is induced while the seed is still on the parental plant combined with the effects of seed environment (Figure 7). In this text, only primary dormancy (from now on dormancy) is being considered.

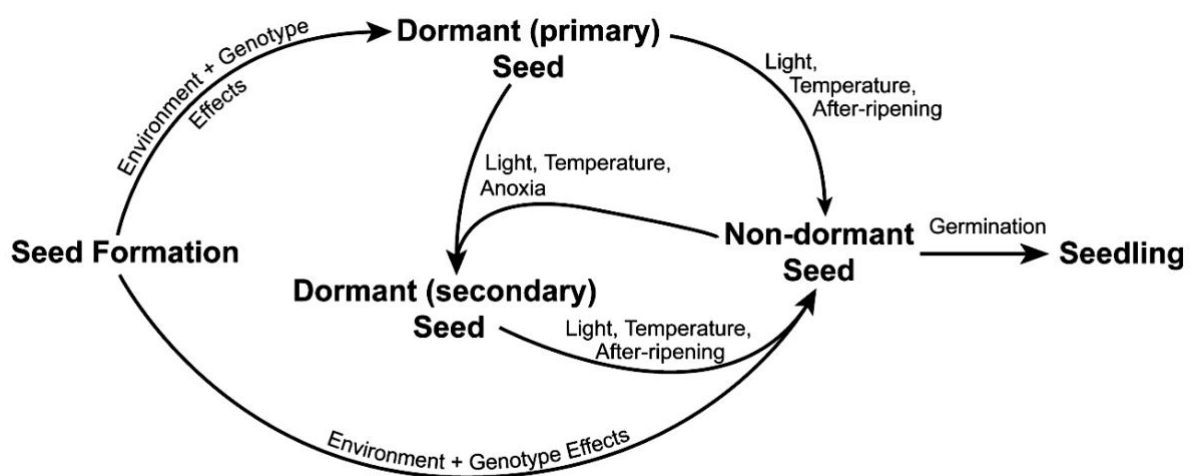


Figure 7. Primary and secondary dormancy – development and factors influencing it (Kermode (2005) from Bewley and Black (1994)).

Dormancy is defined mostly in two ways. First, Bewley (1997) defines it as "*the failure of an intact viable seed to complete germination under favorable conditions*". That is used for example in Dong et al. (2022) or da Silva Alabarce and Dillenburg (2017) or Karimmojeny et al. (2014). This is primary dormancy.

Other studies define dormancy as a state in which a viable seed fails to germinate due to unfavourable conditions, but is still able to germinate if the conditions improve (Leadem, Landis and Thompson, 1997). This is enforced dormancy, used e.g. in Gundel et al. (2009).

Dormancy, like other attributes of germination, is also responsive to TGP, bringing the plants various advantages. Delaying germination by dormancy of some seeds may increase the chances of their establishment in higher population densities, which was also found by Karimmojeny et al. (2014) in a pot experiment conducted on oriental mustard. As mentioned

above, dormancy also helps in regulation of germination timing. That is elaborated e.g. in Lu et al. (2016), a study on *Isatis violascens*, an annual plant. They studied the effects of maturation environment of parental plants on their seeds' dormancy level (and consecutively germination season). They describe that autumn-germinating parents tend to produce seeds with deeper dormancy (germinating in spring, after summer after-ripening and winter cold stratification) than spring-germinating parents, who produce greater proportion of nondeep dormant seeds (germinating usually in autumn, after summer after-ripening). They attribute this TGP to epigenetic mechanisms, but do not explain the particular advantage to the plant. The role of dormancy in connection with parental environment in germination timing is clear nevertheless.

However, dormancy does not always serve parental plants well, as less seeds germinate, so the plants might try to lower its levels. Dong et al. (2022) observed that maternal light environment had effect on dormancy levels of tobacco seeds. Seeds from plants matured in shade expressed lower dormancy than seeds from plants grown in full light, which could be an adaptation of the shaded plants to the discriminative conditions. In a study on *Euterpe edulis* (palm species), da Silva Alabarce and Dillenburg (2017) describe that seeds from trees growing in banana intercrop express higher levels of dormancy compared to seeds produced in native forest. These seeds might be less suitable for further planting, because they take more time to germinate which makes them more vulnerable to predation or damage and it is not advantageous for the crop owners. Both of these cases illustrate that dormancy is not always a desirable trait.

In germination experiments, dormancy and non-viability together contribute to the proportion of ungerminated seeds. A more detailed account of germination percentage is given in the following section.

4.3 Germination percentage

Authors use different terms for germination percentage, for example germinability (Contreras et al., 2008) or germination rate (Guarino et al., 2024), but in the end, they all describe the share of seeds that germinate under given conditions. Ungerminated seeds can either remain dormant and viable or are non-viable. It is worth it to differentiate between the two states, although not all studies do it.

Germination percentage is dependent on the germination environment, but also highly responsive to parental environment transferred by TGP (Sultan, 1996; Contreras et al., 2008; Chen et al., 2020). Both of those are subjected to external stresses like changing temperatures and moisture, light environment or contamination by pollutants or fertilizers. In the following paragraphs, I try to review how different environmental factors and stresses influence

germination percentage through TGP and, where possible, add information whether non-germinated seeds were dormant or non-viable.

4.3.1 Light environment

Parental light environment, especially light quality can have an impact on germination percentage. To exemplify this, Sultan (1996) found that *Polygonum persicaria* seeds from parents grown under low (8%) light had 16% higher germination than seeds from plants grown under full light. Chen et al. (2020) found that soy seeds from plants experiencing shading (intercrop, 60% germination) proved to germinate twice as much as seeds from 'better' light conditions (monocrop, 30% germination). However, reaching contrasting results, Contreras et al. (2008) exposed *Lactuca sativa* maternal plants to long and short days and their seeds to germination tests. Their final conclusion was that it is not the number of hours of light, but the light quality that impacts germination of the seeds. Light quality was higher under short days, due to use of incandescent light for long days and sunlight for short. Hence, germination of long day seeds was lower than that of short day seeds (Figure 8). Seeds from plants experiencing shading (or lower R:FR ratio) usually, but not always, germinate in higher percentages than those from non-shaded plants.

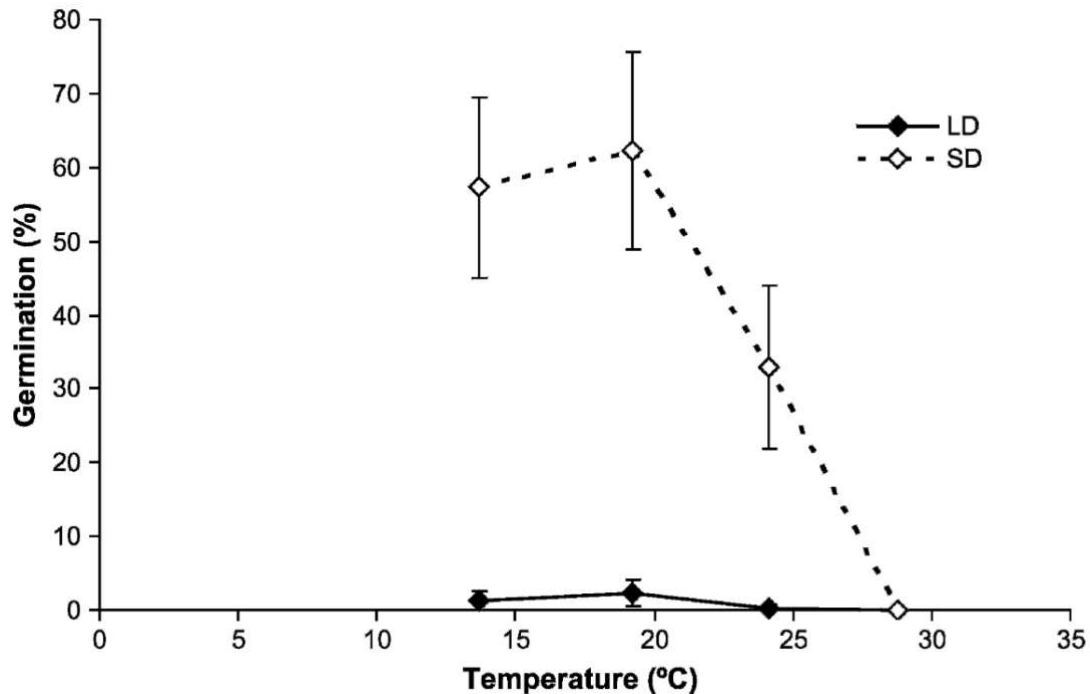


Figure 8. Germination percentage of lettuce seeds under different temperatures; 2 groups of seeds used – from long day (LD) and short day (SD) treated parents (figure taken from Contreras et al. (2008)).

But how does it work? Both Chen et al. (2020) and Contreras et al. (2008) concluded that higher germination percentages under shading (or lower R:FR ratio) are caused by down-regulation of ABA and up-regulation of GA. Contreras et al. (2008) also described that it is caused by the accumulation of phytochrome. It accumulates in the seeds in the form of pre-existent *Pfr*, which is biologically active and mediates seed germination by regulating ABA and GA production. The cultivar Contreras et al. (2008) used is known to be photodormant – the higher temperature, the more photodormant. This would explain the drop of germination percentages in higher temperatures compared to lower temperatures (Figure 8). Based on that presumption, they contemplate that the large difference of germination percentages between long day and short day seeds is caused by higher dormancy of long day seeds. They explain that long days were achieved by incandescent lighting which has higher R:FR ratio than sunlight, so higher dormancy of long day seeds is in accordance with the two statements in the previous paragraph.

4.3.2 Water stress

Water stress in parental environment has usually a negative impact on germination percentage (Pías et al., 2010; Wijewardana et al., 2019), but active response is possible as well (Vander Mijnsbrugge et al., 2023). Wijewardana et al. (2019) tested various levels of soil moisture stress on soybean parental plants and its effects on the progeny. Their conclusion was that the higher moisture stress, the lower germination percentage. Similarly, Pías et al. (2010) found lower germination percentages in seeds from water-stressed parents of *Centrauria hyssopifolia* (gypsophile shrub). Pías et al. (2010) explain this effect as water stress affecting seed provisioning, structure and enzymatic activity influencing germination. Explanation of Wijewardana et al. (2019) is that water stress has a negative effect on embryo growth and development. In contrast, Vander Mijnsbrugge et al. (2023) observed higher germination percentage of seeds from parents experiencing soil moisture stress. They assign it to epigenetic memory. Hostile conditions such as water stress usually have negative impact on seed development, but it can be outruled by epigenetic changes or other active response.

4.3.3 Heavy metals

Heavy metals present a threat to plants by their toxicity, it is therefore a question, how and if they deal with them intergenerationally. Liu, Wolfe and Cobb (2019) grew three generations of rice (*Oryza sativa japonica* Koshihikari) under different copper (CuO) and arsenic (As) concentrations (various combinations between generations) and studied the germination percentage. They observed that the presence of CuO and As alone resulted in lowered germination percentage, whereas in seeds treated with their combination this effect was

mitigated. Subsequently, a study on *Arabidopsis thaliana* by Guarino et al. (2024) examined the effect of acute and chronic parental chromium (Cr) stress on seed germination. They found that even though seeds from non-stressed parents germinated the best under non-stressful conditions, seeds from parents subjected to acute stress germinated better under all stressful scenarios (Figure 9). As shown, TGP is present even for heavy metals with both passive and active response possible.

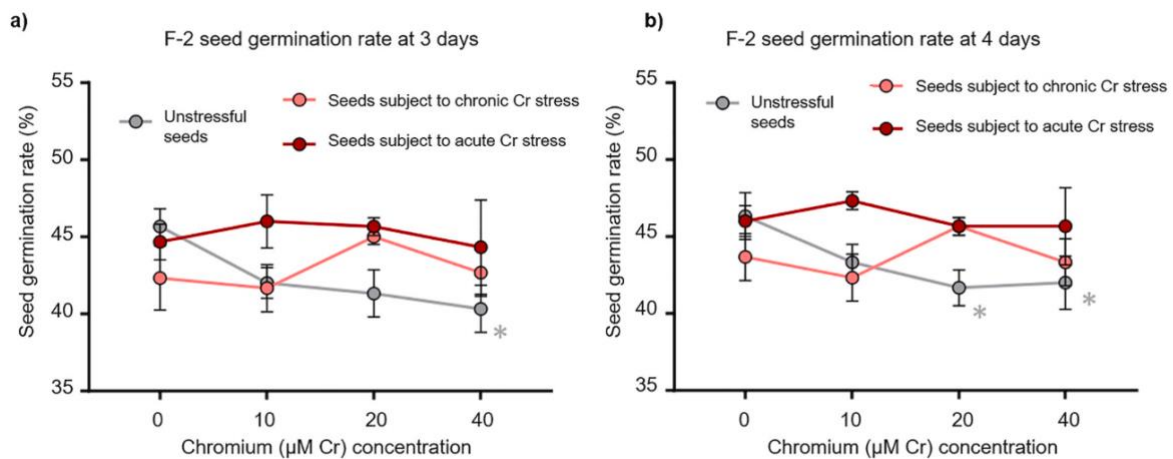


Figure 9. Germination percentage of *Arabidopsis thaliana* seeds from plants kept under acute, chronic or no Cr stress after 3 (a) and 4 days (b) after sowing. Figure taken from Guarino et al. (2024).

4.3.4 Nitrogen

Nitrogen is an important element for plant growth. However, in excessive amounts it can have negative impacts. Seeds of *Taxus baccata* from tree grown in over-fertilized soil, although bigger in size, shown lower germination percentages compared to the ones from non-fertilized tree (Pers-Kamczyc and Suszka, 2022). These seeds also showed higher percent of non-viable seeds among non-germinated ones compared to control and non-fertilized seeds. Bigger size of seeds from fertilized tree did give the emerged seedlings an advantage in performance, but the lower rates of germination could have negative consequences for their regeneration under canopy.

Negative impact is not necessary in all species, though, and can favour certain types of plants. On a pioneer herb *Sinapsis arvensis*, Luzuriaga, Escudero and Pérez-García (2005) found no significant influence of nitrogen addition to the environment of parental plants, as well as Violle et al. (2009) in an experiment on fourteen Mediterranean species without dormancy. Violle et al. (2009) grew plants in monocultures or common garden with either N supply or no fertilization. Luzuriaga, Escudero and Pérez-García (2005) performed the experiment at four sites in field conditions, either with N supply, water addition, their combination, or control with

neither. Comparison of these three experiments shows that some plants can indeed profit from N excess in parental environment which can lead to e.g. spread of invasive species.

4.3.5 Temperature

Baskin and Baskin (2014) summarize that for many species plants grown at higher temperatures have higher germination percentages compared with plants grown in cooler environment. For example, *Arabidopsis thaliana* seeds matured in cold have significantly lower germination percentages compared to those matured in warm conditions (Donohue *et al.*, 2008). However, that is not the case for all species. Li *et al.* (2017) tested germination of seeds from three cultivars of *Vicia sativa* grown either in colder site in higher altitude, or warmer site in lower altitude in China. Ungerminated seeds from all conditions were all viable, but results for the cultivars differed. Two of them expressed no influence of maternal temperature on germination percentage and germinated similarly in all scenarios. Seeds of the third cultivar reacted to the maternal environment. Seeds matured at colder environment had higher germination percentages (than those matured in warmer environment) in lower temperatures and vice versa, showing that the germination response depends not only on species, but also cultivar.

4.3.6 CO₂

Due to human activity the share of CO₂ in the atmosphere has increased. Its levels have impact on seed size/mass, but also germination traits such as percentage. That happens with various results. In a study on *Plantago lanceolata*, Wulff and Alexander (1985) observed increased germination percentage, while Andalo *et al.* (1996) observed its decrease in *Arabidopsis thaliana* (breaking dormancy beforehand), and Steinger, Gall and Schmid (2000) no effect on germination percentage at all on *Bromus erectus*. Plants are able to respond actively to increased CO₂, but it can be a threat to some species.

4.4 Germination time

Germination time is a key factor for successful seedling establishment. If there is no competition, seeds can afford to germinate slower (Chen *et al.*, 2020). Germination time may also increase if seeds are negatively affected by external stresses (e.g. transferred TGP) (Cendán, Sampedro and Zas, 2013). On the other hand, in the case of active answer, if a plant senses cues signalling competition, germination can become faster, so the seeds have a chance to outgrow their competitors (Chen *et al.*, 2020). This section gives examples of both active and passive responses of germination timing to conditions of parental environment, starting with passive answers.

Smaller seeds germinate faster than large ones due to often having thinner coat, and higher surface:volume ratio (Souza and Fagundes, 2014). This is the explanation of a study on *Bromus madritens* and the soil conditions of parental plant on its seeds by Violle et al. (2009). The grass was planted with fourteen Mediterranean annual and perennial species as neighbours (separately). They observed the impact of each neighbour on germination timing of the plant's seeds in two settings – with added and no added nitrogen (N+ and N–; the latter was considered growth-limiting environment). Response of the plant's germination time in N+ treatment did not differ between the neighbours. However, response in N– treatment did differ significantly. Generally, the response was passive and correlated with the ability of certain neighbours to fix nitrogen (N). With neighbours from Fabaceae family, who enrich the soil with N, germination was faster. When N availability in soil was lower, germination was significantly delayed. The authors explain this by changes in mean seed mass. Murali (1997) also found a passive relation of germination timing, their season of flowering and seed size in tropical trees in Southern India. Trees that bear fruits and disperse seeds in dry seasons germinate faster and also have lighter seeds. Generally, the plants want to avoid dispersing seeds in dry season, because they can face desiccation, but compensate it by producing larger quantities. Larger seeds which are more advantageous for establishment of the seedling, but germinate slower, are only possible to be dispersed in rainy season, because they have thicker pericarp and need more water for imbibition. These two studies illustrate that some part of TGP influence on germination time is definitely managed by plants altering seed size.

Let us move on to examples of active responses to conditions of parental environment. Chen et al. (2020) made a study on the effect of growing soybean plants in monocrop versus intercrop. They conclude that seeds from intercrop-grown (shaded) parents germinate faster than those from monocrop (non-shaded) parents (Figure 10). This, along with higher germination percentages (see 4.3 *Germination percentage*) is an advantageous strategy in competitive environments (which shading suggests). Advantages of active responses can also cumulate through multiple generations. Herman et al. (2012) studied the influence of drought stress on germination time across two generations of *Polygonum persicaria*. They found an active response, enhanced when drought stress affected both parental and grandparental generation. Such seeds germinated faster than non-stressed seeds (control). Seeds from stressed parents, but not grandparents, had similar germination time to control and seeds from stressed grandparents and non-stressed parents germinated even slower than control. Herman et al. (2012) explain the fast germination by thinner pericarp (similar as in studies which found passive responses, mentioned above).

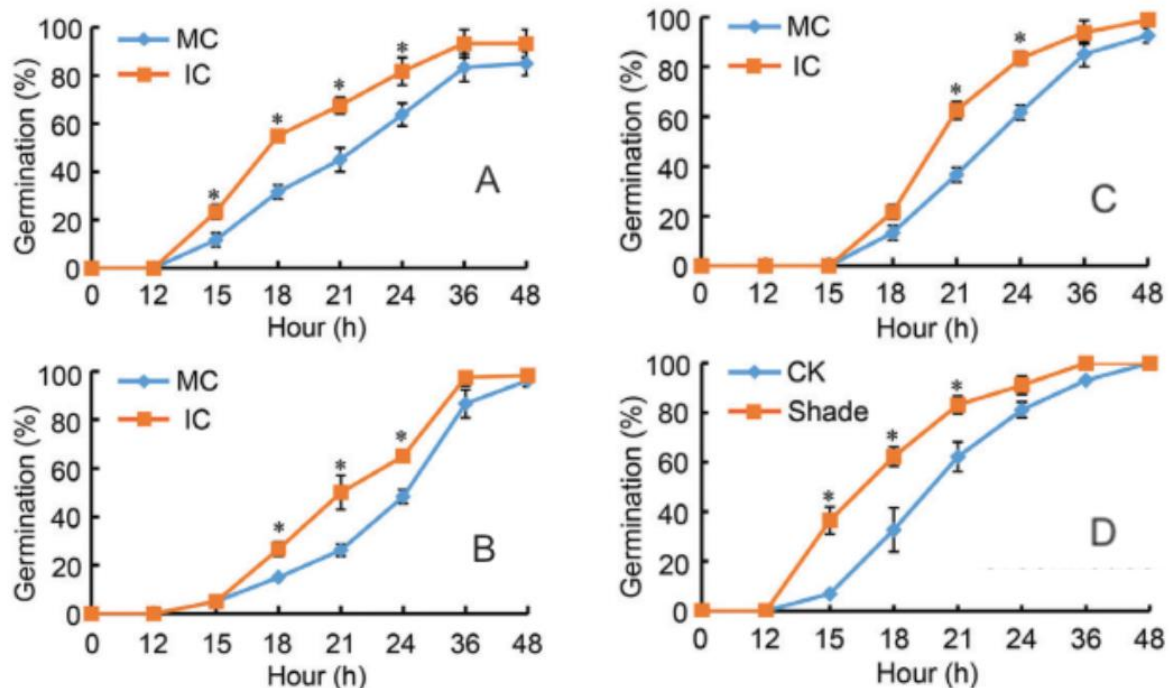


Figure 10. Germination time of seeds from parents grown in monocrop (MS) versus intercrop (IC) (a, b, c) and control (CK) versus shade (d). Used plants were four cultivars of soybean (here a,b,c,d). Figure taken from Chen et al. (2020), modified.

Not all studies go as far as to come to conclusion whether the observed effect was passive or active (see 1. Introduction). Cendán, Sampedro and Zas (2013) show an example of TGP on *Pinus pinaster*. The study examined seeds of trees from two contrasting sites – favourable and unfavourable (higher temperatures and cold springs and autumns, sufficient and insufficient moisture, high and low soil quality). It concluded that seeds from favourable site germinated earlier than those from unfavourable site. The authors write that later germination might help the seeds to avoid cold temperatures of the unfavourable site. However, they say their results are not sufficient to state whether the TGP was advantageous for offspring fitness.

This chapter made an overview of the impact of TGP on various germination traits. Those vary from traits directly connected with germination (germination percentage or time) or its lack (dormancy or seed viability and longevity). Some traits are studied more, most visibly germination percentage. Unlike other traits, the number of studies concentrated on germination percentage was large enough to sort the chapter into categories by types of stress. Nevertheless, all of the traits have impact on subsequent establishment of the seedling and success of population.

Responses to presented stresses are both active – enabling parents to enhance the progeny's wellbeing even when they experienced distress, and passive – simply passing on the distress

or prosperity experienced by the parents. Epigenetic modifications and the content of phytohormones usually mediate active responses and seed provisioning (nutrients) passive. The final type of response differs between species and even cultivars. Even when we compare studies, which subject the plants to similar stresses, their results are often contrasting. Therefore, some of the species are threatened by changing climate conditions such as rising temperatures and drought stress, whilst others adapt better. Among the more adapted species are often found expanding invasive plants with which native plants then have to compete for resources, which also threatens their existence (Luzuriaga, Escudero and Pérez-García, 2005; Violle *et al.*, 2009).

5. Conclusions

Germination is a crucial part of the life cycle of plants and is often affected by transgenerational plasticity. The evoked response can be active or passive. That means, it can potentially enhance the survival of the plant's progeny or deepen the struggles the plant is experiencing. However, sometimes transgenerational plasticity does not have effects at all. From available resources of studies examining it, it does not happen often, but the number of unpublished studies with negative results is not known. Transgenerational plasticity impacts directly the germination and viability of seeds. Subsequently, it influences the survival and spread of plant populations and species and is a widespread phenomenon studied by many.

Different authors label transgenerational plasticity by different names, such as maternal or transgenerational effects. However, transfer of the effects depends both on maternal and paternal plants and sometimes it is not even possible to distinguish between them. Moreover, this thesis describes also the mechanisms which carry on the transgenerational effects. Due to these reasons, transgenerational plasticity seems to be the most fitting name.

Apart from multiple names, transgenerational plasticity was also attributed various mechanisms. The general consensus now is that the two groups are epigenetic modifications and modifications of the seed (seed provisioning and morphological modifications). These mechanisms help to project the quality of soil, water availability, temperature, and light conditions of the parental plants to the traits of their seeds.

The first group, epigenetic modifications are studied less than modifications of the seed, but their research is expanding in recent years. They can be sorted into four groups: (1) nucleosome occupancy and remodelling, (2) RNA interference, (3) relative abundance of histone post translational modifications and (4) cytosine (DNA) methylation. An interesting example of epigenetics as a mechanism is a study by Alsdurf, Anderson and Siemens (2016) which found a trade-off between drought tolerance and herbivory defense in *Boechera stricta*, showing that epigenetics can cause multiple effects at once. Else, epigenetic modifications usually mediate active responses and their effects also persist through multiple generations. This, combined, is very advantageous for the plants.

The second group of mechanisms, modifications of the seed are abundantly studied, both morphological modifications and amount of stored resources. Stored resources in the seed fall under two categories – nutrients and other compounds. Their effects are summarized below. The content of nutrients in seeds depends on their availability to the parental plant and usually mediates passive responses. Nutrients serve the emerging seedling as base source of energy before it is able to gain its own resources. So more provisioned (i.e. larger) seeds are usually more desired. Although not always. Sometimes plants trade quality (fewer large seeds) of the

seeds for quantity (more smaller seeds) to ensure success. Smaller seeds tend to germinate and spread faster, which is advantageous in competitive environments.

Other compounds in the seeds are mainly phytohormones, RNAs and transcription factors, secondary metabolites, and symbionts. The phytohormones abscisic acid and gibberellins are crucial for germination. The former inhibits germination, the latter promotes and they both crosstalk with other phytohormones causing various effects. An important factor for regulation of the effect of phytohormones is shading, which often decreases or increases the concentrations of abscisic acid and gibberellins in the seeds.

Second group of other compounds – RNAs and transcription factors, also regulate dormancy and germination. Through transgenerational plasticity, they are able to induce for example resistance to chromium stress leading to higher germination percentages. They usually mediate active responses and are often tied to epigenetic modifications of the seed.

Third group – secondary metabolites and symbionts (fungi and bacteria) transferred from maternal plant to the seed are studied very scarcely. Nevertheless, they do have a role in transgenerational plasticity. They bring the seed numerous advantages when non-stressed (resistance to herbivory or drought), but e.g. under ozone stress have a negative influence on the seed's welfare. Symbionts stored in seeds are the only mechanism linked only with negative impact on germination (from found studies).

The most frequently studied morphological modification is thickness of pericarp. Pericarp is a maternal tissue, so the plant has an inherent influence on it. Pericarp thickness often affects germination time, because seeds with thin pericarp germinate faster than seeds with thick pericarp due to easier water intake at imbibition and emergence of the radicle.

Mechanisms described above mediate the influence of transgenerational plasticity on seed viability and longevity, percentage of dormant seeds, germination percentage and time. The seeds that successfully survive and break dormancy make for the germination percentage. That is the most abundantly studied aspect of germination, although not evenly for all the conditions. There are numerous studies on parental light environment, but for example the effects of CO₂ concentrations in the atmosphere could be studied much more. The effects of transgenerational plasticity on germination percentage differ between species and even cultivars. This happens in studies concentrating on all kinds of parental conditions – light environment water stress, nitrogen and fertilization, temperature, and CO₂. Worth noting is that in the case of water stress, active response occurred only when the mechanism of transgenerational plasticity were epigenetic modifications. Similarly to that, epigenetics were also helping to achieve an active response of seeds from plants exposed to chromium stress. These studies exemplify that epigenetics can help plants creating resistance leading to higher germination percentages.

Apart from germination percentage, another important aspect is the time of germination. Germinating faster than competitors can ensure seed's easier access to resources needed for seedling establishment and subsequent growth. Hence, in competitive environments, plants sometimes prefer smaller seeds over large. Even though small seeds store less nutrients critical for initial growth of the seedling, they germinate and spread faster and can sometimes outcompete others nevertheless. Notable is a study of Herman et al. (2012) who described that active responses of transgenerational plasticity can cumulate over multiple generations and seeds of both stressed parents and grandparents germinated better than control or seeds from only one stressed generation.

Sometimes, seeds are not able to survive difficult conditions and some part of them ends up non-viable. Distinguishing dormant and non-viable seeds among ungerminated adds important information to germination studies. However important, viability is usually only an additional part of studies which concentrate on germination percentage or longevity. Longevity is the time period for which the seeds are able to stay viable. An important condition of parental environment affecting seed longevity is temperature. Under low temperatures, some studies report decrease of seed longevity, others increase. As well as in the case of germination percentages, the effects of transgenerational plasticity on seed longevity vary between species. Knowing how long the seeds of different species can survive in nature or be stored is important for their protection or future reintroductions.

In case the seed does not germinate, but is viable, it is probably dormant. Dormancy helps seeds wait for suitable conditions for germination, an advantageous trait to many plants. However, when dormancy percentages are too high, it might not be an advantageous trait anymore. This happens for example when plants are grown in monocultures (non-shaded environment) rather than in their native environment (native forest with more shade) (da Silva Alabarce and Dillenburg, 2017). Dormancy exposes the seeds for longer period to predators and other damage, lowering the seeds' chances to establish successfully.

Generally, the effects of transgenerational plasticity on germination differ between species and cultivars. Even though there are some patterns, there is not one utterly clear for any of observed parental conditions or mechanisms. It is important to know, whether species are able to adapt to the rapidly changing environmental conditions and succeed. Invasive species are traditionally able to respond actively to changing condition and outcompete native species. Knowledge of the effects of transgenerational plasticity on seed germination can help controlling species survival or reintroduction and may be helpful to study more.

6. Bibliography

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