REVIEW

Climate change affects seed aging? Initiation mechanism and consequences of loss of forest tree seed viability

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Abstract

Key message Environmental stress resulting from rapid climate changes leads to the initiation of the seed aging process in mitochondria and peroxisomes. Seed storage methods limiting germinability loss are fundamental for forest future.

Abstract Seed aging is a natural process. It decreases the seed germination rate, i.e. the process is essential for the plant's life cycle. Aging involves a progressive accumulation of oxidative damage over time. One of the main plant responses to stress is an excessive production of reactive oxygen species (ROS), such as $O_2^{\bullet}$, H_2O_2 and $^{\bullet}OH$. If the concentration of ROS is too high, it causes damage of the structure of lipid membranes, proteins, carbohydrates, and DNA. Climate changes affect tree reproduction and may have long-term consequences in the form of reduced species dispersal and acquisition of new habitats. High temperatures accelerate the aging of seeds and decrease their viability. There is, therefore, an indisputable need to store forest reproductive material to maintain continuity of regeneration in farm forests. The quality of seeds subjected to long-term storage correlates negatively with ROS concentration, as ROS accumulation typically occurs in tissues experiencing oxidative stress. Therefore, to preserve forest genetic resources, it is particularly important to know the causes and sites of initiation of the aging process in seed cells, as well as to prevent the germination rate decrease by developing appropriate storage methods. The main organelles responsible for intracellular ROS production are mitochondria and peroxisomes. This article aims at verifying the causes of seed aging and determining its consequences for future forest regeneration due to climate changes. We review the literature on oxidative stress, as well as the sites where the tree seed aging process originates, such as mitochondria and peroxisomes.

Keywords Seeds aging · Climate change · Reactive oxygen species · Antioxidants system · Mitochondria · Peroxisomes

Introduction

The seed is the first developmental phase and the basic form of adaptation of higher plants to surviving in unfavorable environmental conditions. It is the role of seeds to transfer features to offspring, in other words, to guarantee the continuity of species (Kurek et al. 2019). Seeds tend to age, just like any other plant organ (Lehner et al. 2008). The process reduces plant's ability to germinate, which is the essential role of seeds in the life cycle of plants (Jiménez-Alfaro et al. 2016). The viability of seeds is modified by various factors like: (1) internal physiological and biochemical (Hu et al. 2012a) that depend on the species and are genetically conditioned (Becerra-Vázquez et al. 2018), and (2) external, such as moisture and temperature conditions of storage of seeding material (Pukacka and Ratajczak 2007). In the "free-radical theory" of aging, Harman (2006) assumed that aging is a progressive process of the accumulation of oxidative damage, induced by oxidative stresses of various origins that gradually increase the risk of death of all living organisms.

Throughout their long lives, trees are exposed to various kinds of stress (Kijowska-Oberc et al. 2020). It may be caused by unfavorable external conditions, such as water shortage, extreme temperatures, strong salinity or too high levels of toxic metals (Siripornadulsil et al. 2002).

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Depending on the inducing factor, stress may restrain plant development to a different degree at the various phases of its life (Hayat et al., 2012). One of the main responses of plants to stress is an excessive production of reactive oxygen species (ROS), such as $O_2^{-\bullet}$, H_2O_2 and $^\bullet OH$ (Das and Roychoudhury 2014; Kurek et al. 2019; Huang et al. 2019). High concentrations of ROS cause damage by inactivating enzymes, disturbing the structure of lipid membranes, proteins carbohydrates and DNA (Sharma et al. 2012; Silva et al. 2018).

Climate change, which affects the reproduction of trees, may have long-term consequences by reducing species dispersal and by the acquisition of new habitats (Dyderski et al. 2018; Wang et al. 2019; Bogdziewicz et al. 2020). Therefore, there is an indisputable need to store forest reproduction material to guarantee the continuity of regeneration of species in farm forests. Trees produce more flowers at higher temperatures but the flowers are not effectively pollinated and numerous seeds are infertile as a result (Pearse et al. 2016). Global warming influence on the reproductive effort of forest trees, that display masting—the synchronized production of large amounts of seeds, but the specific impact is still difficult to assess (Caignard et al. 2017). High temperatures of air are recognized by trees as a signal to get ready to produce more seeds; this is termed the "seeding year" (Koenig et al. 2016). On the other hand, heavy-seed species need a couple of years to recover the energy, indispensable for producing flowers and fruit in high numbers again, and this results in desynchronized seed yields (Monks et al. 2016). Observations conduced in the recent decades revealed a relationship between the increase in average temperatures and higher frequency of seeding years in European beech (*Fagus sylvatica* L.) (Bogdziewicz et al. 2020), temperate oaks (sessile oak—*Quercus petraea* (Matt.) Liebl. and pedunculated oak—*Quercus robur* L.) (Caignard et al. 2017).

Most species have clearly recalcitrant or orthodox seeds. However some species with recalcitrant seeds can significantly change their position on the desiccation tolerance scale depending on climate (Daws et al. 2006). Climate changes occur at a rate that is too fast to enable genetic adaptation of such species, and thus these plants may have a considerable influence on the ability of their seeds to germinate (St Clair and Lynch 2005). Desiccation tolerance, such as other plant features, is shaped under the environmental conditions by phenotypic plasticity (Fang et al. 2017; Solarik et al. 2018) and it may affect the limits of species natural ranges (Dobrowolska 2015; Cavin and Jump 2017). Daws et al. (2006) proved that recalcitrant seeds of sycamore (*Acer pseudoplatanus* L.) can move from one seed storage category to the next under the impact of climate changes. They showed that seedlings from warmer locations in Europe (France and Italy) were more desiccation tolerant than those from cooler locations (Norway and Scotland), therefore environmental conditions during seed development systematically affect seed features including the level of seed desiccation tolerance. Those observations have supported the work of Walters et al. (2005), who found that seeds from warm, arid environments have the ability to withstand long-term storage in contrast to seeds derived from temperate and moist regions.

Research of Pukacka et al. (2003) indicate that the reduced viability of the seeds of European beech after being stored for 10 years correlated positively with increased concentrations of ROS and lipid peroxidation products, the accumulation of which is typically observed in tissues under oxidative stress conditions. During the long-term storage, the redox state in cells of beech seeds significantly changes and it may resulting in intensifying the process of aging, which leads to the reduction of seed viability (Ratajczak et al. 2019c). Maintenance of the redox status balance in cells of seeds has a considerable impact on the preservation of seed viability during drying and storage (Ratajczak et al. 2019a). Reproduction plays the key role in populations survival, thus it should be taken into consideration during modeling responses of populations to climate change (Morin et al. 2008; Dyderski et al. 2018). Therefore, for the preservation of the gene resources of forests, it is of particular importance to understand the causes of aging and the sites of its initiation within seed cells, as well as to prevent the loss of germination by developing appropriate seed storage methods.

Mitochondria and peroxisomes are the main organelles responsible for the intracellular production of reactive oxygen species (Cabiscol et al. 2013; Liberatore et al. 2016; Ratajczak et al. 2019b). One of the sources of ROS is the mitochondrial electron transport chain that generates $O_2^{-\bullet}$. Plant peroxisomes produce mainly H_2O_2 (Luis et al. 2006). In this paper, we attempted to identify the causes of seed aging and the consequences of climate change with reference to guaranteeing the appropriate seeding reserves for the purpose of forest regeneration in the future. With this in mind, we made a survey of the literature on oxidative stress as well as the sites where seed aging is initiated, such as the mitochondria and peroxisomes, in the seeds of trees.

Reactive oxygen species vs. sensitivity of plants to stress

The extent of seed damage during storage depends on their specific characteristics and requirements (Walters et al. 2005; Rajjou et al. 2008; Sano et al. 2016). Drought is a stress factor reducing metabolic activity, but reduced water content is required et several phases of the development, such as seed desiccation (Leprince et al. 1999). Based on

these, seeds are classified into three categories: orthodox, recalcitrant and intermediate. Orthodox seeds acquire desiccation tolerance, therefore they are prepared for survival in unfavorable environmental conditions even during development. This adaptive strategy is a result of sugar, heat shock proteins (HSPs) and late embryogenesis abundant proteins (LEAs) syntheses (Berjak et al. 2007). However, recalcitrant seeds cells do not contain those components and the lack of them leads to membrane damage and, as a consequence, to viability loss due to environmental stress (Black et al. 2006). Recalcitrant seed may lose viability during long-term storage because of water content remaining high during their development until germination (Walters 2015).

Under favorable conditions ROS levels are effectively controlled. They occur as regulators in process of cell growth and development of tissues, in photosynthesis, respiration and cell cycle (Buetler et al. 2004). Stress factors disturb redox homeostasis, resulting in excessive accumulation and decreased elimination of ROS, which leads to the oxidative stress state (Noctor et al. 2018). The oxidative stress occurring in seed cells contributes to deterioration of the seeding material. This state is generated by disturbances of an equilibrium of the system protecting the cells from excess ROS (Demidchik 2015; Huang et al. 2019). The ROS comprise superoxide anion radical $O_2^{-\bullet}$ and hydrogen peroxide H_2O_2, as well as free radicals (oxygen-based and organic), including highly reactive hydroxyl radical $\bullet OH$ (Kumar et al. 2015). These molecules contain unpaired electrons and react readily with proteins, lipids and nucleic acids. The hydroxyl radical $\bullet OH$ is the most aggressive form of ROS: it causes structural damage in deoxyribose, pyrimidines and purines (Cadet et al. 2017). The concentration of ROS varies during the whole life of seeds. During the development of Norway maple seeds, H_2O_2 potentially plays a signaling role in acquisition of desiccation tolerance (Ratajczak et al. 2019a). Orthodox seeds of this species acquire water stress tolerance as a result of intracellular modifications, e.g. accumulation of lipids and starches, the presence of heat shock proteins (HSPs) and late embryogenesis abundant proteins (LEAs), improving cell mechanical resilience and facilitating storage in a dry state conditions (Waterworth et al. 2015; Kubala et al. 2015). The reason why the recalcitrant and the intermediate seeds are less viable after being desiccated and stored is that ROS are produced in excess in response to the stressful conditions. Furthermore, they are accumulated and not removed as effectively as in orthodox seeds, because of lower activity of several elements of the antioxidant system, such as glutathione (GSH), ascorbate (ASC) (Ratajczak et al. 2015) or LEAs, which have been shown to be critical for desiccation tolerance (Delahaie et al. 2013).

During storage, the level of ROS in the seeds will grow, affecting their viability and germination ability (Bailly and Kranner 2011; Parkhey et al. 2012; Gomes and Garcia 2013;

Jeevan Kumar et al. 2015). This happens because the ROS cause a number of unfavorable changes in the cells which, in turn, affect the quality of seeds during storage and their viability (Fig. 1). Peroxidation (1), i.e., oxidation of lipids, is one of the main causes of deterioration of the seeding material (Parkhey et al. 2012). The process affects the components of the cell membranes, disturbing their selective permeability (Ratajczak et al. 2015). It also disturbs the performance of the antioxidant system enzymes (Pukacka and Ratajczak 2007). Carbonylation of proteins (2), during which carbonyl groups are formed in the radicals of some amino acids, may result in modified conformations, followed by changes in or loss of some of the functions of the proteins (Dalle-Donne et al. 2003; Kalemba and Pukacka 2014). The number of cracks in the DNA helix or single thread grows higher with the seed age and the associated increase in ROS concentration (3), often leading to chromosomal aberrations (Waterworth et al. 2015). Moreover, malonaldehyde—the product of a reaction between oxygen radicals and the cell membrane lipids—may react with nitrogen bases of DNA (Marnett 1999; Grotto et al. 2009). All these processes decrease the seed viability.

Antioxidant system in seed cells

The extent of damage taking place in the seed cells is correlated with the efficiency of the enzymatic and non-enzymatic elements of their antioxidant systems (Bailly 2004). The function of these systems is to eliminate oxidative agents, but also to maintain redox equilibrium (Foyer and Noctor 2005; Dietz and Hell 2015; Noctor et al. 2018).

The enzyme-based antioxidant system comprises a number of enzymes: superoxide dismutases (SOD), peroxidases (POX), catalase (CAT), ascorbate–glutathione cycle enzymes, and proteins comprising thiol groups such as peroxyredoxins (Prxs) (Fig. 1). The superoxide dismutase neutralizes the superoxide anion radical $O2^{-\bullet}$ to hydrogen peroxide H_2O_2 and oxygen (Wang et al. 2018). Catalase (CAT) neutralizes hydrogen peroxide (Apel and Hirt 2004) and is present mainly in peroxisomes and glyoxysomes (Ighodaro and Akinloye 2017). CAT is a verified indicator of improvement of the seed quality and germination ability (Kibinza et al. 2011). Plant cells commonly comprise the glutathione, guaiacol and ascorbate peroxidases that catalyze the decomposition of hydrogen peroxide. Oxidative damage of cells is also prevented by the alternative peroxidase (AOX) (Selinski et al. 2018). PRXs mentioned above are enzymes that neutralize hydrogen peroxide (Foyer and Noctor 2005). They have a number of important functions, for instance, they control cell signals and the redox condition in plant cells. This way, peroxyredoxins help plants adapt to new environmental conditions (Dietz 2011; Liebthal et al. 2018). Their application may improve the seed tolerance
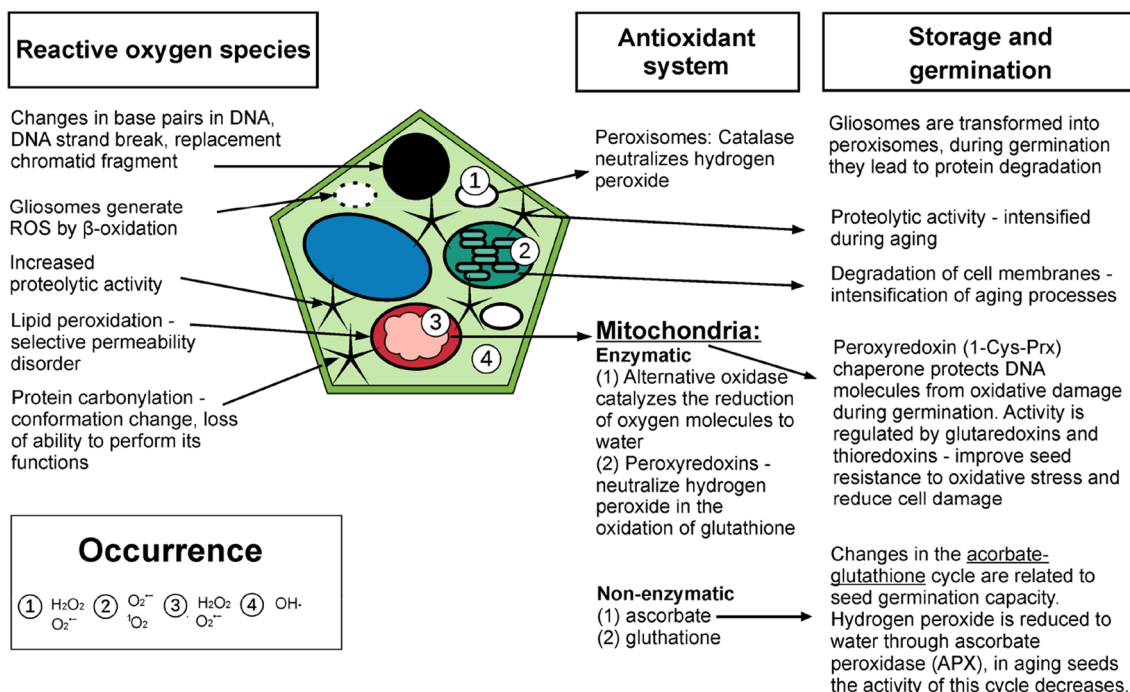
Fig. 1 The activity of reactive oxygen species and components of the antioxidant system affecting seeds quality during long-term storage and seed germination in plant cell

to oxidative stress and diminish cell damage (El-Maarouf-Bouteau and Bailly 2008; Xie et al. 2019).

The non-enzymatic components of the antioxidant system include low molecular compounds: ascorbic acid (its reduced form ASA and oxidized form DHA), and glutathione (its reduced form GSH and oxidized form GSSG) (Mittler et al. 2004; Kranner et al. 2006; Xia et al. 2015). These low molecular antioxidants cooperate in the Halliwell-Asada cycle (ascorbate–glutathione cycle, ASC-GHS cycle), and changes in its activity affect seed germination (Fig. 1) (Pukacka and Ratajczak 2007). In the seeds of European common beech after aging, the concentration of ASA in samples stored for 2 years decreased twice as much as that in the seeds stored for 5 years, and the level of GSSG was higher than that of GSH, indicating the oxidative stress condition in the seeds. This means a positive correlation between germination and the content of ASA and GSH in the seeds (Pukacka and Ratajczak 2007).

Seed aging initiation sites

Mitochondria

The mitochondria are the essential sources of energy for cell growth and metabolic activity. Being one of the main sites of ROS production, these organelles are also responsible for maintaining cell redox equilibrium (Ratajczak et al. 2019b). The mitochondrial ROS are mainly generated in complex I and complex III of the mitochondrial electron transport chain (Barranco-Medina et al. 2007; Robb et al. 2018), from which $O_2^{-\bullet}$ molecules are released into the matrix, and in complex II during the reverse transport of electrons to complex I (Blokhina and Fagerstedt 2010). Decomposition of $O_2^{-\bullet}$ produces H_2O_2, which has the ability to freely pass through the cell membranes. It reacts with $O_2^{-\bullet}$ generating a highly reactive $^{\bullet}OH$, and its reaction with NO produces the powerful oxidant $ONOO^-$ (Belhadj Slimen et al. 2014). The mitochondria comprise proteins which take part in the formation of ROS such as glycerophosphate dehydrogenase (Drahota et al. 2002, Murphy 2009), pyruvate dehydrogenase complex with many subunits, as well as the structurally membrane-bound complex of α-ketoglutarate dehydrogenase (Starkov et al. 2004).

ROS disturb the integrity of membranes and other cell components (Dunn et al. 2015). Under oxidative stress, the activity of mitochondrial proteins is reduced due to binding the lipid peroxidation products (Winger et al. 2007), the formation of carbonyl groups (Kristensen et al. 2004) and oxidation of tryptophan radicals (Møller and Kristensen 2004). In the seeds of trees of the genus elm (*Ulmus* L.), 48 mitochondrial proteins were transformed during aging and it was confirmed that these changes were linked to the mitochondrial electron transport chain and to the Krebs

cycle (TCA)—the basic path of aerobic respiration (Li et al. 2017). Oxidative phosphorylation is one of the main sources of ROS in cells. Combined with the "free-radical theory" (Harman 2006), which describes aging as an accumulation of free radicals, it gives grounds for believing the theory correctly describes mitochondria as the seed aging initiation sites (Ratajczak et al. 2019b).

Seed aging has a direct impact on the effectiveness of the electron transport chains by reducing ATP production. Therefore, the aging seed cells are not capable of releasing enough energy stored in ATP to initiate germination. Stress in the mitochondria triggers energy deficit signals (Liberatore et al. 2016) in the form of changes in the ROS level and the mitochondrial redox condition, which in turn affect the expression of mitochondrial and nuclear genes controlling seed aging (Yin et al. 2016). Changes in the mitochondrial redox condition control not only the mitochondrial activity but also various processes taking place in the cells, such as seed germination (Nietzel et al. 2020) or activation of apoptosis (programmable cell death) (Rouhier and Jacquot 2005).

Peroxisomes

Peroxisomes are eukaryotic organelles in which H_2O_2 production and decomposition take place. These molecules are neutralized by CAT, called the marker protein for peroxisomes, in which the enzyme constitutes up to 25% of total protein content (Corpas et al. 2001). In this way, these organelles help control the redox condition in addition to being important generators of molecular signals (Corpas et al. 2001). In photosynthesizing tissues, the essential task of peroxisomes is their role in photorespiration (Hu et al. 2012b). On the other hand, glyoxysomes—the category of peroxisomes that are present in seeds—take part in ROS production by β-oxidation of lipids. This is a process that enables the mobilization of storage material in the form of lipids, which are accumulated in the endosperm during the seed maturation. After being transformed into sugars, the lipids are oxidized, generating metabolically useful energy (Graham 2008). Moreover, germination inhibitors may become neutralized during β-oxidation, which interrupts the seed dormancy phase (Footitt et al. 2006).

The seed aging process is accompanied not only by enhanced lipid peroxidation but also by an increase in proteolytic activity (Distefano et al. 1999). Proteolysis is the process in which peptide bonds are disrupted by proteases. It helps maintain an equilibrium between the biosynthesis and the elimination of the exhausted cell components (Hu et al. 2012b). Proteolysis is indispensable during germination, morphogenesis and apoptosis (Palma et al. 2002). The process is related to oxidative stress: the rate of proteolysis is higher in cells exposed to stressogenic factors (Pyngrope et al. 2013) because intracellular proteins, damaged by ROS

molecules, are identified and selectively decomposed by endopeptidases (Grune et al. 1997). Proteolytic activity was observed also in the peroxisomes. The transformation of glyoxysomes into leaf peroxisomes during germination as well as the reverse process implies the degradation of previously existing proteins in these organelles (Nishimura et al. 1996).

Summary: global warming vs. the quality of the seeding material

The frequency of extreme weather conditions, such as hurricanes but also droughts and heat waves (Easterling et al. 2000) grows as the result of high atmospheric CO_2 levels, among other things. In 2015, CO_2 level exceeded 400 ppm for the first time since its monitoring has begun (Jones 2017). Climate conditions changes in recent years are noticeable (Fig. 2) and they have an impact on seeds, contributing directly and indirectly to deterioration of their quality, vitality and quantity. High air temperature in the year predicting the "seeding year" is recognized by trees as a signal to abundant flowering and high seed production next season (Koenig et al. 2016). However the improving performance of trees during the increase of mean air temperature is only an apparent phenomenon, because increased seed production is accompanied by a decrease in the synchrony of reproduction (Bogdziewicz et al. 2020). It is a result of the need for several years of energy regeneration necessary to produce such a large number of reproductive organs and fruits (Monks et al. 2016).

Stress, the plant response to unfavorable environmental conditions, makes the plants produce too much ROS. As the result of excess ROS, the plant DNA and proteins are damaged, which disturbs the seed maturation process. In effect, seed aging is induced too early for them to maintain their high quality and enable the desirable breeding effects to be obtained in the future (Fig. 3). In 2018, an experiment was carried out in which individuals representing 17 tree species were made to germinate and grow at controlled conditions, at temperatures and CO_2 levels above natural (Kim and Han 2018). The experiment proved that long-term exposure of seeds to high temperatures not only affected their ability to germinate but also disturbed their dormancy, resulting in reduced activity of hormones and enzymes, and all this induced germination. In another study extensive sets of tree reproduction data for sessile oak and the pedunculate oak was analyzed to determine whether seed production had changed over the last two decades in response to global warming. Monitoring of seed production was carried out for 14 years in 28 forests of both tree species distributed throughout France. These analyses showed significant

Fig. 2 Changes in the maximum, minimum and mean temperatures, and mean precipitation in subsequent months in 2016, 2017, 2018 and 2019 seasons in Kórnik, Poland (data from meteo station)
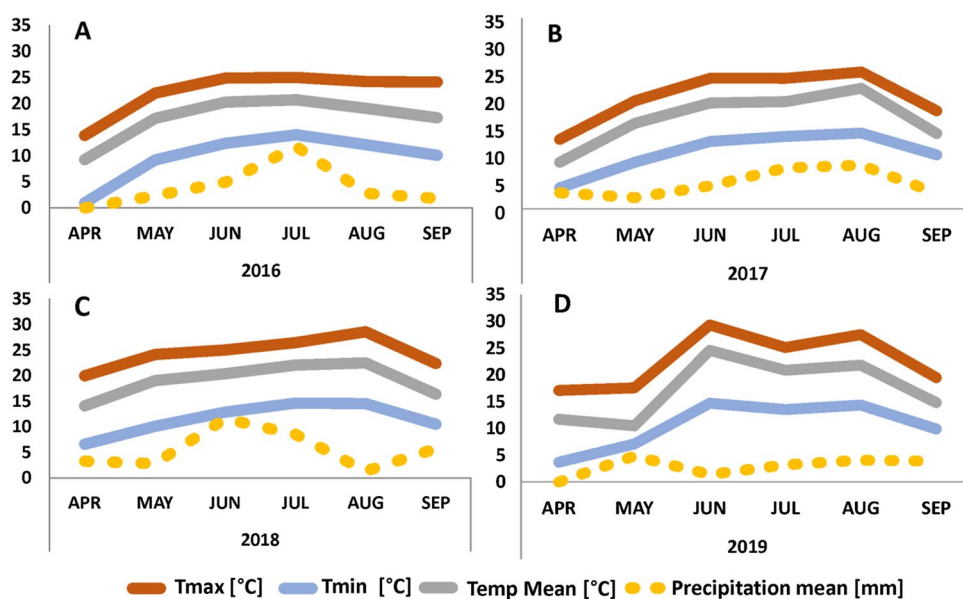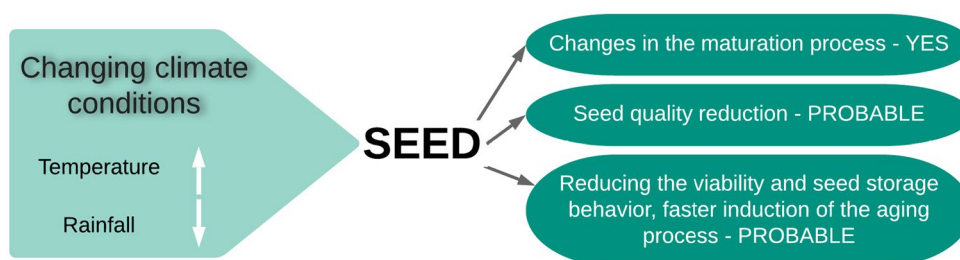

Fig. 3 Impact of changing climatic conditions on the quality and viability of forest reproductive material, current knowledge and perspectives

temperature-induced trends in seed production (Caignard et al. 2017).

Desiccation tolerance may be a hereditary trait while desiccation sensitivity is environmentally determined (Dickie and Pritchard 2002; Oliver et al. 2000). Therefore the loss of desiccation tolerance results vitality predominance, as desiccation-sensitive species, contrary to species with high desiccation tolerance, directly commit fewer resources to mitigate seed predation by faster germination. In dryland habitats with sporadic rainfall they have a number of adaptations that reduce the loss of seed viability and maintain their high quality. In these species, shedding occurs at the time of maximum annual rainfall (1), they produce seeds of large weight (2) to reduce the rate of seed drying and they are also characterized by rapid germination (3), which allows them to reduce seed dehydration (Pritchard et al. 2004). Desiccation sensitivity and other traits of specific species may form a continuum of responses in relation to maturation status (Daws et al. 2004). For instance, sycamore (*Acer pseudoplatanus* L.) seeds can shift their seed storage category depending on climate (Daws et al. 2006), while seeds of *Trichilia emetica* Vahl., tropical African forest species, tolerate elevated temperature or even such thermal conditions may to

increase germinability (Sershen et al. 2014). Environmental conditions during seed development affect the seed features such as their level of desiccation tolerance. For example, a promising indicator of oxidative stress levels changing due to thermal or drought stress may be proline, which reaches higher levels in more sensitive to environmental stress, recalcitrant seeds (Kijowska-Oberc et al.—research under revision). For this reason, it is important to take into consideration the species provenance during the characterization of seed desiccation tolerance and other responses.

The indirect effect of global warming on seeds is connected with their long-term storage. Desynchronization of massive seed yields for trees exhibiting cyclic yields results in a lower number of seeds with a living embryo (Bogdziewicz et al. 2020). Under the circumstances, it becomes indispensable to secure the seeding material by storing it after harvesting for the purpose of forest regeneration in the future. However, seeds with lower tolerance affected by high temperatures and water deficit in the maturation phase may rapidly loose viability during long-term storage (Fig. 3). Understanding how those changes affect seed quality and desiccation tolerance may be crucial for protecting the genetic resources of forest species. Meanwhile, research

on the impact of climate change on the aging process of seeds usually concerns herbs (Davies et al. 2013; Willis et al. 2008), rather than woody plants. Minimization of the risk of seed aging initiation will help maintain their quality and viability. Germination ability is a fundamental value in forest cultivation as it ensures the continuity of forest ecosystems.

Compliance with ethical standards

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