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A FOREST STARTS WITH SEEDS

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Focus on Reproductive Biology

The role of seeds is crucial in tree production and development, and the future of forests depends on them. But what impact is climate change having on the seed life cycle? Will the trees that grow out of them manage to survive and adapt to the new environment?

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orests cover nearly 31 percent of the Earth's total land area, with the number of trees recently estimated at 3 trillion $(3 \times 10^{18}!)$. Forests significantly contribute to sustaining life on Earth, including providing a source of livelihood for people, clean air and water, and preserving biodiversity. Old, species-diverse forests can mitigate the impact of negative climate change on the functioning of ecosystems, not just forest-related ones. Protecting existing biodiversity in forests is necessary for preserving the genetic resources capable of ensuring the continuity and sustainability of ecological processes and maintaining biodiversity (including at the genetic, species and ecosystem level) for future generations.

How does a species-diverse forest emerge?

The life cycle of each plant begins with seeds and is dependent on their production in subsequent planting

cycles. The quality, shape and sustainability of our forests depend to a large extent on the seeds used for afforestation and renewal, processes mainly conducted by humans. They are collected by foresters from specially selected sections of the forest (forest stands). In light of current regulations, conservative forest stands play a special role, as due to their age they are considered to be best adapted to the environmental conditions in a given area. Despite this, according to the latest scientific reports, the state of the oldest stands is declining, as climate change affects environmental conditions both in Poland and worldwide. Environmental changes are happening at an unprecedented pace and have a significant impact on the quality of seeds produced by these age-old forest stands, which in the future may lead to the disappearance of valuable genotypes and, as a consequence, a more radical reconstruction of our forests. This is a bigger problem, because with the strong impact of climate change on seeds and thus the reproduction of old trees, we could be faced with the disappearance of highly specialized species and genotypes, with low genetic variability and poor phenological plasticity.

Physiological reprogramming

Despite their seemingly simple structure (consisting of an outer cover, storage tissue, and an embryo), seeds are receptacles of the richness of future generations of a given species, and are the key to its adaptation and



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survival in a changing environment. Sudden changes in ecosystems pose a threat to seed quality, and thus to the sustainability of many plant species in their present location. It is seeds that determine whether a given plant species will manage to "emigrate" in the event of adverse conditions. For trees that do not complete their life cycle in a year or two, the seeds produced may not be able to keep up with rapid environmental changes.

Seed production by woody plants depends on many factors, including insolation, water and wind conditions, the presence of pollinators, the occurrence of diseases and pests in the trees that produce them, but above all temperature and humidity. These two factors most strongly affect all stages of seed development, from pollination through ripening and dormancy, to their germination in the future. By 2100, global temperature is predicted to increase by a further 2°C. Extreme weather conditions, including heat waves and longer periods of drought occurring during the flowering period and later, when the seeds ripen on the tree, directly affect the nature and quality of the seeds produced. Even seemingly small changes in seed maturation, weight or size can affect their fate. One example is reduced seed size. Smaller seeds are easier to spread, but on the flip side their ability to germinate and the speed at which that happens, as well as the further growth of seedlings, may be very limited. This will affect entire populations and ecosystems in the long run. Disturbances during seed maturation can significantly impact seed durability, resistance to drying, as well as the physiology of seed dormancy.

Seed dormancy is a condition when seeds do not germinate, despite the presence of favorable conditions. The phenomenon is closely related to the climate in which the plant grows, because seed germination and seedling survival depend on seasonal weather changes. Depending on the type of dormancy, it may be interrupted by factors including damage to the impermeable seed coat (as in the black locust), a period of warmer temperature (as in the European ash) or, as in most cases, low temperature (in apple or beech trees). The breaking of dormancy allows germination to occur in optimal conditions for seedling growth. Previously, environmental conditions matched the requirements of seeds, providing the right amount of coldness in autumn and winter necessary to interrupt seed dormancy. The temperatures that can effectively trigger the interruption of physiological dormancy of seeds depend on the species and may have a wide (0-15°C) or very narrow (2-4°C) range. Today it is estimated that winters in Poland will have significantly fewer days with temperatures below freezing, and the average temperature in January may rise by up to 5°C. This poses a threat to seeds requiring long periods of low temperatures to break their dormancy. If it is not fully broken, the seeds will not germinate in spring, although they may well survive in the soil until the following winter (creating a seed bank). Among the important tree species that shape Poland's forests, the ones most endangered are beech, ash, hornbeam, rowan, maple, sycamore, and wild fruit species that constitute an important biocenotic admixture for forests.

Similarly, the germination time of non-dormant seeds (such as oaks) may also be affected. Dormant seed germination is expected to accelerate when temperatures rise in colder regions. However, in regions with dry climate zones, seeds exposed to low temperatures will start to germinate late due to insufficient moisture. There are concerns that germination times, altered due to temperature and humidity changes, will not be synchronized with the most favorable time for growth. Seedlings formed in the warmer winter months will still be exposed to regular freezing and thawing during early spring frosts, and above all to increased competition, because moderate warming will promote seed germination and seedling production in many species at the same time.

The impact of climate change on seed germination is a complex and still poorly researched problem. However, global warming directly affects water availability and average temperatures, the two factors that primarily control the growth and regeneration of trees. A warmer environment will positively affect the seed germination process itself, but extreme warming may cause their viability to deteriorate. The key question is whether warming will push species far beyond their optimal temperature range. There are two possible scenarios. In the first, the small and gradual change in global temperature will be outside, but still close to the optimum temperature, which will result in increased production of heavier seeds. This will increase the fertility and germination of seeds and accelerate the growth of seedlings. However, if the temperature suddenly rises far beyond the optimum, plants will produce small seeds in smaller numbers, whose germination rate will be low, and the emerging seedlings weak and few. This negative scenario has one positive outcome, which is that it will bolster the territorial spreading of species.

Adaptation and protection

Tree development processes, such as seed maturation, the breaking of dormancy, and germination require the accumulation of a specific number of degree-days (°D), calculated as the total duration of effective temperatures necessary for these processes to occur. Phenological models help determine the thermal threshold that enables vegetation to start and the number of degree-days required to move into subsequent development phases. The amount of warmth necessary to

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trigger the transition to the next stage of development depends on the species, but also from plant to plant. Such intra-species variability of allows for a certain "plan of action" to acclimatize to a new environment in the long run. This depends on both genetic diversity and phenotypic plasticity. It is thanks to the latter variability that plants adapt faster to the environment, as opposed to genetic diversity.

Seeds accumulate in their phenotypic memory (through epigenetic changes) the history of the thermal conditions in which their parents grew, adding to it the thermal conditions in which they themselves will need in order to effectively coexist with the environment after being released from the mother plant. Such memory should allow seeds to adapt their germination phenology to climate change, as increasing ambient temperatures can reduce the time of the cool stratification needed to break dormancy and trigger seed germination. Such thermal memory stays in seed-producing plants for years, and it moreover continues in subsequent generations. This suggests that plants should be able to adapt to the slow increase in average temperatures being caused by climate change. However, this conclusion applies to the most genetically diverse populations. Local varieties, best suited to their original locations, may have a much more specific character and not cope with environmental change as well.

Protecting the genetic resources of such varieties and stands from disappearing from a given environment in the long run will preserve greater adaptability and protect biodiversity. The Kostrzyca Forest Gene Bank was established near Karpacz in the Karkonosze Mountain region in order to protect genetic resources in *ex situ* conditions. The seeds of woody species, herbaceous plants, as well as smaller and larger shrubs that form the forest undergrowth are collected and stored there under controlled conditions. It is one of few such gene banks in the world, where seeds of forest species, dried to appropriate moisture levels and kept in sealed containers, are stored at -20° C or in liquid nitrogen (-196° C).

Sensing the right moment

A ripening seed, which will immediately free itself from the mother plant, is a new living being that has a much greater potential for escaping danger as compared to its parents, and a much greater survival potential than the entire plant. The goal of seed physiologists is to develop basic models that can comprehensively predict seed responses and strategies in a changing environment. On one hand, we ask ourselves questions about the direction of climate change, on the other, we ponder how seed production will change under these new conditions. How far will they be spread from the mother plant? How deep will their



dormancy be? When will they germinate? How many seedlings will they eventually produce?

For seed scientists, plant biologists, and scientists dealing with global climate change, understanding all these factors is just the beginning of being able to predict the behavior of seeds in response to the changing temperatures inside them. Such research will hopefully allow us to determine and describe the critical temperature thresholds within the short life of seeds, beyond which plant reproduction in a changing environment may be disturbed. There are many indications that the physiological and biochemical mechanisms of various plants and seeds will allow them to survive climate change. But what about trees? Will they be able to adapt? Can older stands that are not able to adapt to new environmental conditions nevertheless still produce good quality seeds? Many more aspects of this topic still remain to be studied much more thoroughly.

Seeds come in diverse forms and types: small and large, recalcitrant and orthodox, light and heavy... How will they adapt in response to climate change?

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