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INFLUENCE OF EXTERNAL FACTORS ON SEED GERMINATION IN FIELD CROPS

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Abstract

Seed germination is a complex biological process influenced by a combination of internal and external factors. This paper analyzes the impact of key environmental factors: temperature, water availability, light, pH value, and storage conditions on seed germination, with a particular focus on field crops. Temperature plays a crucial role in enzymatic activity and metabolic processes, with both excessively high and low temperatures negatively affecting germination due to oxidative stress and enzyme inhibition. Water availability is essential for seed rehydration and metabolic activation, while excess moisture can lead to anaerobic conditions that hinder germination. Light influences germination through photoreceptors that regulate hormonal balance, affecting dormancy and growth initiation. Soil pH affects nutrient availability and enzyme activity, with extreme pH levels inhibiting seed metabolism. Finally, storage conditions determine seed viability over time, with high humidity and temperature, accelerating biochemical degradation. Understanding these factors is crucial for optimizing seed germination and improving agricultural productivity, particularly in the context of climate change.

Key words: seed germination, temperature, water availability, light, pH, storage conditions, oxidative stress

Introduction

Seed germination depends on a combination of internal (endogenous) and external (exogenous) factors. Internal factors include the genetic and physiological traits of the seed, while external factors, such as temperature, moisture, and light availability, play a crucial role in the germination process. These factors can act individually, but their effects depend on their interactions (Long et al., 2015). Water availability, temperature, light, and oxygen presence collectively regulate the seed's metabolic activities and determine the dynamics of seedling emergence. Research shows that a combination of genetic characteristics and environmental conditions can break seed dormancy or stimulate germination, allowing plants to adapt to changing ecological conditions (Finch-Savage and Footitt, 2017; Golijan et al., 2021; Golijan et al., 2022). The temperate continental climate of Serbia is becoming increasingly extreme, with greater temperature fluctuations in winter, more frequent floods, dry and hot summers, and arid autumns. As a result, agricultural producers must adapt crop production to changing environmental conditions (Vrbničanin et al., 2015). Unfavorable environmental conditions, such as extreme temperatures, drought, or excessive moisture,

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can slow down or completely inhibit germination, significantly impacting agricultural systems and natural ecosystems (Finch-Savage and Bassel, 2016). Understanding the impact of these factors is essential for improving sowing techniques, optimizing crop yields, and adapting agricultural production to the challenges of climate change.

This paper analyzes the influence of key external factors on seed germination, with a focus on field crops, considering relevant scientific literature in the fields of seed physiology and agricultural technology.

The influence of water on seed germination

Water is a key factor in the process of seed germination, as it enables the rehydration of the seed's dry matter, the activation of enzymes, and the initiation of metabolic processes necessary for seedling growth. The germination process begins with imbibition, or water uptake, which leads to seed swelling and activation of cellular functions (Upretee et al., 2024). During imbibition, water penetrates the seed coat and enables the hydration of macromolecules such as proteins, lipids, and carbohydrates, which is crucial for restarting metabolic activity in the seed. Hydration activates enzymes, softens cell walls, and restores the structure of organelles, allowing for cell expansion and the beginning of embryo growth. Simultaneously, imbibition softens the seed coat, increasing its permeability to oxygen and dissolved nutrients, which further supports germination. This physiological phase represents the first and essential step in reactivating seed metabolism after dry dormancy.

Water availability directly affects seed metabolism by initiating enzymatic reactions needed for the breakdown of storage reserves. Starch, proteins, and lipids serve as the main energy sources in the seed, and their hydrolysis into simpler molecules such as sugars and amino acids supports cell division and radicle elongation. Enzymes such as amylase, protease, and lipase play a key role in this phase, as they convert stored macromolecules into energy forms usable for early seedling development (Finch-Savage and Bassel, 2016). In maize (*Zea mays* L.), water stress during early developmental stages significantly reduces germination, attributed to the inhibition of enzymatic activity and decreased energy synthesis (Khaeim et al., 2022a). Similarly, wheat (*Triticum aestivum* L.) seeds require an optimal moisture level to activate amylase and break down starch. Therefore, insufficient or excessive moisture can lead to reduced germination due to disturbances in amylase activation and the creation of anaerobic conditions (Khaeim et al., 2022b).

A lack of water can significantly delay or completely inhibit seed germination, as water is essential for initiating the metabolic processes required for germination. Under drought conditions, seeds often remain dormant or exhibit incomplete germination, resulting in weak and underdeveloped seedlings with reduced survival capacity. Water stress disrupts cell turgor pressure, limiting cell expansion and impairing DNA replication and protein synthesis, which are essential for seedling establishment (Saux et al., 2020). Additionally, low water levels can reduce the efficiency of hormonal signaling pathways, particularly those involving gibberellin (GA), which promotes germination, and abscisic acid (ABA), which maintains dormancy. Seeds under drought stress may exhibit elevated ABA concentrations, further inhibiting germination and delaying emergence (Nambara et al., 2020). Soybean (*Glycine max*), as a legume with a hard seed coat, shows high sensitivity to drought, leading to increased levels of abscisic acid and negatively impacting germination. However, seed treatments such as priming with potassium nitrate or salicylic acid improve seed response to drought stress by reducing oxidative damage and positively influencing hormonal balance (Miladinov et al., 2019).

On the other hand, excessive moisture can create anaerobic conditions in the soil, reducing the availability of oxygen necessary for embryo development. Oxygen is required for aerobic respiration, the process through which adenosine triphosphate (ATP), the cell's energy currency, is produced. In saturated soil conditions, oxygen diffusion is limited, forcing the seed to rely on anaerobic respiration, which produces less ATP and results in toxic byproducts such as ethanol and lactate. These compounds can cause metabolic disorders, leading to seedling abnormalities or complete germination failure (Pan et al., 2020). The optimal moisture level required for germination varies among plant species and depends on seed coat permeability, storage conditions, and the presence of dormancy mechanisms. Seeds with hard or impermeable seed coats, such as legumes, often require scarification or extended imbibition to allow sufficient water penetration. In contrast, seeds with thin or permeable seed coats, such as grasses, absorb water more quickly and initiate germination earlier. Environmental factors, such as soil texture, humidity, and temperature also influence water availability and thereby affect the germination rate.

Understanding the role of water in the germination process is crucial for optimizing agricultural production, especially in the context of climate change, which affects water availability in the soil. Rising temperatures and unpredictable rainfall patterns can lead to prolonged droughts or excessive precipitation, posing significant challenges to crop establishment (IPCC, 2021). Strategies such as seed priming, irrigation management, and soil moisture conservation techniques can help mitigate the negative effects of water stress on germination and improve seedling survival rates. Seed priming methods, such as hydropriming, osmopriming, and chemical priming, have been proven to enhance germination and drought resistance in various plant species. Future research should focus on identifying drought-tolerant seed varieties and optimizing water use efficiency to improve germination success under variable climatic conditions. The development of drought-tolerant varieties and effective water management strategies is essential for sustainable agriculture in the face of climate change (Marthandan et al., 2020).

The influence of temperature on seed germination

Temperature is one of the key factors influencing various physiological processes in seeds, including germination. On a chemical level, temperature affects the rate of enzymatic activity responsible for breaking down the seed's energy reserves, as well as the stability of biochemical molecules. At optimal temperatures, enzymes that break down starch and other storage materials operate at maximum efficiency, enabling rapid and successful germination. However, excessively high or low temperatures can disrupt these processes, reducing the rate and success of germination (Sharma et al., 2022). At low temperatures, enzymatic activity decreases, reducing the efficiency of metabolic reactions necessary for germination. This can lead to slower germination, weaker radicle development, and, in extreme cases, complete germination failure.

On the other hand, high temperatures trigger a series of biochemical changes that can be harmful to seeds. Increased temperature leads to increased production of reactive oxygen species (ROS), such as superoxide ($O_2\bullet-$) and hydrogen peroxide (H_2O_2). These molecules can cause oxidative stress, damaging essential biomolecules such as lipids in cell membranes, proteins, and DNA. Oxidative stress results in structural and functional changes in these molecules, negatively affecting the overall integrity of the seed and its germination capacity. In response to oxidative stress, plants increase the activity of enzymes that neutralize ROS, such as superoxide dismutase (SOD) and catalase (CAT). SOD catalyzes the dismutation of superoxide radicals into hydrogen peroxide, which is then broken down by CAT into water and oxygen, forming the first line of defense against ROS. However, if ROS production exceeds the capacity of these enzymes to neutralize them, oxidative stress ensues, which can cause damage to lipids, proteins, and DNA, reducing seed vitality and the ability of seedlings to survive under unfavorable conditions (Pinheiro et al., 2023).

High temperatures can also accelerate protein denaturation, compromising the function of enzymes and other vital molecules within the seed. At the molecular level, protein denaturation can alter their structure and function, reducing their ability to perform key biochemical processes necessary for germination. Considering all these factors, germination is most successful when temperature maintains a balance between adequate enzymatic activity and minimized oxidative stress. Therefore, optimal temperature conditions are crucial for seed germination and plant development (Sharma et al., 2022).

Studies have shown that different plant species have different responses to temperature conditions during germination. For example, a study on the effect of temperature on germination of legume grain seeds (*Pisum sativum* L., *Phaseolus vulgaris* L., *Vicia faba* L., *Glycine max* L.) showed that the optimal temperature for germination of most of these species is 25°C. However, a temperature of 20°C negatively affected the germination energy and germination rate of pea, bean, and faba bean seeds, while the temperature had a positive effect on both seed quality indicators for faba bean, winter pea, and soybean. Low temperatures during germination can cause significant damage to legume grain crops, as germination energy was 0% for most species, and the germination rate was very low (Rojnica et al., 2022).

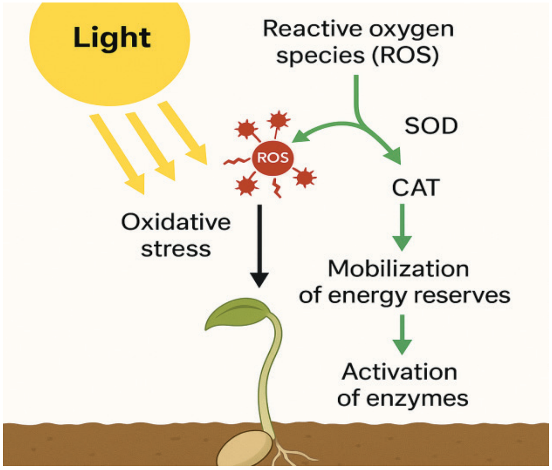
Studies on Phacelia (*Phacelia tanacetifolia* Benth.) have shown that storage temperature significantly affects seed dormancy duration. Seeds stored at 20°C lose dormancy faster compared to seeds stored at 5°C. Complete loss of dormancy was recorded after 56 days of storage at 20°C, while at 5°C, it took 70 days (Đukić, 2017). Temperature significantly affects corn growth and yield, with high night temperatures reducing the number of kernels per ear (Hatfield, 2016). Also, the study by Khaeim et al. (2022a) found that temperatures above 30°C negatively affect corn seed germination and seedling growth. According to the research by Haj Sghaier et al. (2023), the optimal temperature for sunflower germination is around 25°C, while temperatures above 35°C significantly reduce germination rate. Additionally, Knežević et al. (2023) found that the highest germination was achieved at 30°C, while lower temperatures slowed germination. The optimal temperature for wheat germination is between 20°C and 25°C, achieving the highest germination percentage and rate, while high temperatures above 30°C negatively affect seedling growth and induce oxidative stress (Sharma et al., 2022). The study by Asseng et al. (2015) showed that an increase in temperature by 1°C can reduce wheat yield by about 6%, with germination being particularly sensitive to high temperatures during early developmental stages.

The influence of light on seed germination

Light plays an essential role in regulating seed germination through the activation of photoreceptors such as phytochrome and cryptochrome, which initiate a series of signaling pathways necessary to trigger metabolic processes. Red light converts phytochrome from its inactive form (Pr) to the active form (Pfr), thereby stimulating the biosynthesis of gibberellic acid (GA), a hormone that promotes the breakdown of starch reserves into sugars and initiates germination. Conversely, far-red light shifts phytochrome back into its Pr form, decreasing GA synthesis and increasing the concentration of abscisic acid (ABA), which prolongs seed dormancy (Shu et al., 2016).

Light of different wavelengths has varying effects on plants at different developmental stages. Red light stimulates seed germination by activating phytochromes that trigger biochemical processes which break dormancy and promote growth. In contrast, blue light and conditions with a low red to far-red light ratio (R/FR) can inhibit germination, signaling shaded conditions that may not be suitable for seedling establishment. Both red and blue light play key roles in the de-etiolation process of seedlings, which includes the transition from skotomorphogenesis (growth in darkness) to photomorphogenesis (growth under light). Red light promotes stem elongation and chlorophyll synthesis, while blue light affects phototropism, stomatal opening, and the development of more compact and robust seedling structures (Vinković et al., 2017).

At the molecular level, light not only regulates hormonal signals but also induces the production of reactive oxygen species (ROS), which play a dual role in the germination process. While ROS can cause oxidative stress, their controlled accumulation acts as a signal for cell wall degradation and the activation of enzymes involved in reserve mobilization. The activation of antioxidant systems, including enzymes such as superoxide dismutase (SOD) and catalase (CAT), enables the maintenance of redox balance and protects seedling cells from damage. These light-induced chemical changes contribute to the effective mobilization of energy reserves and the initiation of embryo growth (Farooq et al., 2021) (Picture 1).



Picture 1. Effects of light on seed germination and the associated biochemical changes
Slika 1. Efekat svetlosti na klijanje semena i vezane biohemijske promene

Research has shown that LED lighting with different spectral compositions significantly affects germination and early development of field crops. For example, in wheat, the combination of red and blue light increases photosynthetic activity, tiller number, and total biomass, while a high proportion of blue light prolongs the juvenile phase and improves the plant's antioxidant capacity (Blidar et al., 2021). In rice, exposure to blue LED light results in broader leaf width and increased dry mass, while red light promotes stem elongation. These morphological changes are associated with the activation of specific photoreceptors and hormonal pathways that regulate growth and development (Ren et al., 2023). Similarly, in oats, the application of LED lighting with a high blue-to-red light ratio shortens stem length and accelerates heading time, which is beneficial for selecting cultivars adapted to controlled growing conditions (Rybka et al., 2020).

A study conducted by Vinković et al. (2017) showed that LED lighting increases the germination of lamb's lettuce (*Valerianella locusta*) compared to fluorescent light. This effect may be related to improved conditions for activating enzymes necessary for the breakdown of starch and other energy reserves in the seed. The results of the study indicate that the type of lighting significantly affects the germination energy and final germination rate of lamb's lettuce seeds, which were considerably higher under LED lights, while germination energy and final germination of garden cress seeds were not dependent on light type. A similar effect of light on seed germination was documented in a study by Poplašen et al. (2019), who examined the photomorphogenesis of lamb's lettuce under different light spectra. This study showed that prolonged exposure to various types of light can significantly enhance germination, especially under controlled light cycle conditions. Luković et al. (2024) note that during early seedling production in December, January, and February, when sunlight quality and duration are inadequate, energy-efficient LED lights can meet the plants' light requirements during early development stages, enabling effective organogenesis throughout growth.

On the other hand, a study by Vrdoljak (2015) investigated the effect of LED lighting on the germination of carrots and spinach, showing that this type of lighting positively influences germination speed and uniformity. These results indicate that light, particularly in the form of LED lighting, can have a significant positive effect on seed germination, with potential applications in agriculture and horticulture.

The influence of pH on seed germination

The pH value of the soil or substrate significantly affects seed germination, as pH regulates the availability of nutrients and the activity of enzymes involved in the breakdown of the seed's energy reserves. Research has shown that the activity of α-amylase, a key enzyme for starch hydrolysis, is highest at pH values between 5 and 6, which allows for efficient starch breakdown and the release of sugars needed for energy during germination. In contrast, at pH values below 4 and above 7, α-amylase activity is reduced, which can limit energy availability and slow down germination (Figure 1). Extreme pH values can also directly affect seed coat softening and destabilize enzymatic activity during germination, particularly enzymes with amylolytic activity. These pH-induced changes can lead to disruptions in the catabolism and reutilization of the seed's nutrient reserves, negatively impacting the germination process. Additionally, extreme pH values can cause physical changes in the seed coat and destabilize the enzymatic system, including enzymes with amylolytic functions, further impairing reserve catabolism and the germination process (Agić et al., 2009). Extreme pH levels can also cause oxidative stress in the seed, leading to the accumulation of reactive oxygen species (ROS) and damage to membranes, proteins, and DNA, further reducing the seed's germination potential (Wang et al., 2024).

The explanation: The diagram includes the optimal pH range for enzyme activity, such as α-amylase, as well as the negative effects of extreme pH values on enzymes, membrane structures, and oxidative stress. Optimal activity occurs within the pH range of 5–6, while extreme pH values reduce enzyme activity, which can negatively impact energy availability and germination rate.

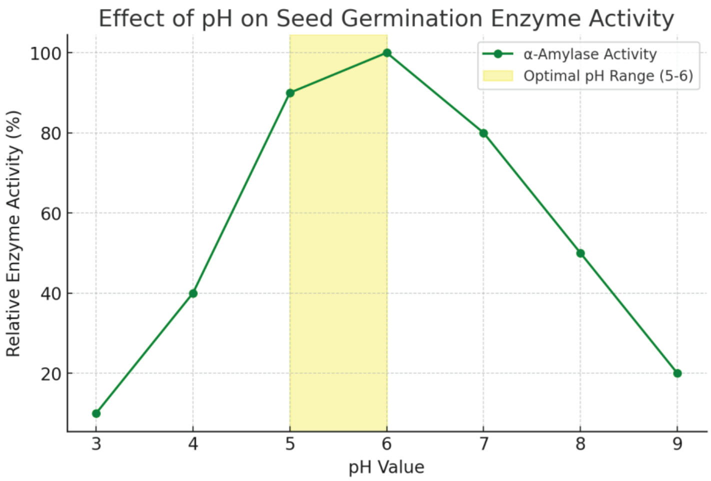


Figure 1. Effect of soil pH on seed germination
Grafikon 1. Efekat pH zemljišta na klijanje semena

Studies have shown that pH values between 6.0 and 7.0 provide optimal conditions for the germination and early development of maize, with the highest germination rates and best root system development recorded. A decrease in pH below 5.0 or an increase above 8.0 results in reduced germination and seedling viability. Tolerance to pH stress varies among maize genotypes (Mandić et al., 2023). The optimal pH for wheat germination is between 6.0 and 7.5. pH values below 5.0 or above 8.0 can negatively affect seed germination and seedling growth, reducing germination energy, root length, and shoot freshness. Wheat's resistance to pH stress depends on the variety and specific soil conditions (Liu et al., 2022).

Sunflower grows best in soils with pH values between 6.5 and 7.5. Studies have shown that pH values below 5.0 or above 8.0 negatively affect seed germination, reducing germination energy and root length. Resistance to pH stress depends on the cultivar and soil conditions (Loose et al., 2017).

The influence of storage conditions on seed germination

Seed storage conditions, including temperature, humidity, and light exposure, play a crucial role in preserving seed germination capacity. During storage, seeds undergo various biological and chemical changes that can reduce their ability to germinate. On a chemical level, in dry storage conditions, seed metabolism slows down, reducing the activity of enzymes responsible for the breakdown of energy reserves, such as amylase and lipase, which helps maintain seed dormancy. However, under humid conditions, increased enzyme activity can lead to faster depletion of reserves and reduced germination capacity (Wang et al., 2018). Higher temperatures accelerate the respiration process, increasing the production of reactive oxygen species (ROS), which can cause oxidative stress and damage molecules such as lipids, proteins, and DNA, thereby further decreasing seed germination ability (Ratajczak et al., 2019). High relative humidity causes lipid peroxidation and degradation of cell membranes, while elevated temperatures accelerate protein breakdown, reducing the availability of amino acids for early embryo development. Storing seeds at lower temperatures slows down these harmful processes and helps preserve the seed's metabolic activity (Silva et al., 2023). Various storage conditions can induce chemical stress in seeds, affecting their long-term viability and germination potential (Marcos-Filho, 2015). Poor storage conditions can also lead to ROS accumulation, negatively affecting cellular components and reducing the seed's ability to maintain vitality during long-term storage (Kurek et al., 2019). A study conducted on five maize lines showed that prolonged storage periods negatively affect germination and seedling characteristics. Seeds stored at 22°C and 60% relative humidity exhibited a decrease in germination and germination energy over time, with different lines showing variable resistance to storage conditions (Muleta, 2022). The study found that storage conditions at 20°C and 60% relative humidity, using airtight packaging, were the most favorable for maintaining the physiological quality of sunflower seeds over a six-month period. Higher temperatures had a negative impact on germination, while different packaging types showed varying efficiency in preserving seed quality (Coradi et al., 2015). Table 1 shows the impact of storage conditions on seed germination in selected plant species.

Conclusion

External factors such as temperature, water availability, light, pH levels, and storage conditions significantly influence seed germination by affecting its metabolic and biochemical processes. These factors regulate enzymatic activity, oxidative stress levels, protein stability, and

Tabela 1. Klijavost semena (%) povrtarskih vrsta nakon uvoza i nakon 20 meseci skladištenja u kontrolisanim i nekontrolisanim uslovima izražena kao srednja vrednost +/- standardna devijacija.
Table 1. Seed germination (%) of vegetable species after import and after 20 months of storage in controlled and uncontrolled conditions, expressed as a mean +/- standard deviation.

Vegetable species	**Germination after import (%)**	**Germination in CSC (%)**	**Germination in UCSC (%)**
Apium graveolens var. secalinum L	81±1.63 [a]	43±1.83 [b]	28±2.16 [c]
Apium graveolens L	81±1.41 [a]	0±0.50 [b]	0±0.00 [b]
Petroselinum crispum ssp. *crispum* L	67±1.83 [a]	22±3.65 [b]	5±1.83 [c]
Spinaca oleracea L	84±1.83 [a]	43±1.83 [b]	44±2.58 [b]
Capsicum annum L	73±1.83 [a]	63±2.94 [b]	60±1.83 [b]
Allium porum L	77±3.56 [a]	30±2.58 [b]	32±3.16 [b]
Vicia faba L	95±1.83 [a]	46±2.71 [b]	46±1.41 [b]
Brassica oleracea var. capitata L	80±2.16 [a]	76±1.83 [b]	65±1.63 [b]
Brassica oleracea var. italica L.	82±2.58 [a]	81±1.83 [a]	59±1.83 [b]
Latuca sativa L	93±1.83 [a]	80±3.65 [b]	49±2.16 [c]
Beta vulagris subsp. vulgaris var. conditiva L	82±2.58 [a]	57±2.58 [b]	15±2.58 [c]
Daucus carota L	84±3.16 [a]	73±2.16 [b]	79±3.37 [c]
Valerianella locusta (L.). Laterr.	87±2.58 [a]	78±1.83 [b]	72±1.83 [c]
Cichorium endivia L	90±1.83 [a]	85±3.65 [b]	82±2.94 [b]
Cichorium intybus L	90±1.83 [a]	87±1.83 [a]	89±2.94 [a]
Pisum arvense L	96±1.83 [a]	85±2.94 [b]	88±2.58 [b]
Phaseolus vulgaris L. ssp. vulgaris var.nanus f. fibriferis	89±1.82 [a]	87±2.94 [a]	89±3.65 [a]
Cucurbita pepo L	97±1.83 [a]	93±1.83 [b]	83±2.58 [c]
Cucumis sativus L	97±0.82 [b]	99±0.82 [a]	96±1.41 [b]
Solanum melongena L	89±1.83 [b]	94±2.94 [a]	81±2.16 [c]
Citrulllus lanatus (Thunb) Matsum. et Nakai	95±2.16 [b]	100±0.00 [a]	95±0.82 [b]
Cucumis melo L	83±3.16 [b]	93±3.37 [a]	88±1.83 [ab]
Lycopersicon esculentum Mill	86±2.58 [a]	88±1.83 [a]	87±1.63 [a]
Phaseolus vulgaris L. *ssp. vulgaris var. nanus f. sine fibris*	88±2.58 [a]	91±1.83 [a]	76±4.40 [b]

CSC - controlled storage conditions; UCSC - uncontrolled storage conditions; Results are expressed as meanvalue ± SD (n=4); statistically significant difference at $p<0.05$; Source: Horvat et al. (2020).

hormonal balance, ultimately determining seed viability and seedling development. Optimizing germination conditions is essential for achieving high agricultural yields and ensuring crop adaptability to changing environmental conditions. Future research should focus on developing strategies to enhance germination under diverse agroecological conditions, contributing to sustainable agricultural production.

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Author contributions

Conception and design of the study: J.G.P., G.M, A.P., S.M.; Analysis and interpretation of data: J.G.P., G.M, A.P., S.M.; Visualization: J.G.P.; Writing manuscript: J.G.P., G.M, A.P., S.M.

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UTICAJ SPOLJAŠNJIH FAKTORA NA KLIJAVOST SEMENA RATARSKIH USEVA

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Sažetak

Klijanje semena je složen biološki proces koji zavisi od kombinacije unutrašnjih i spoljašnjih faktora. Ovaj rad analizira uticaj ključnih ekoloških faktora – temperature, dostupnosti vode, svetlosti, pH vrednosti i uslova skladištenja na klijavost semena, sa posebnim osvrtom na ratarske useve. Temperatura ima ključnu ulogu u enzimatskoj aktivnosti i metaboličkim procesima, pri čemu i previsoke i preniske temperature negativno utiču na klijanje usled oksidativnog stresa i inhibicije enzima. Dostupnost vode je neophodna za rehidrataciju semena i aktivaciju metabolizma, dok višak vlage može dovesti do anaerobnih uslova koji ometaju klijanje. Svetlost utiče na klijavost putem fotoreceptora koji regulišu hormonalnu ravnotežu, utičući na dormanciju i početak rasta. pH vrednost zemljišta utiče na dostupnost hranljivih materija i aktivnost enzima, pri čemu ekstremne pH vrednosti mogu inhibirati metabolizam semena. Na kraju, uslovi skladištenja određuju dugoročnu vitalnost semena, pri čemu visoka vlažnost i temperatura ubrzavaju biohemsku degradaciju. Razumevanje ovih faktora ključno je za optimizaciju klijanja semena i unapređenje poljoprivredne produktivnosti, posebno u uslovima klimatskih promena.

Ključne reči: klijavost semena, temperatura, dostupnost vode, svetlost, pH, uslovi skladištenja, oksidativni stress

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