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Review

Responses of Soybean to Selected Abiotic Stresses—Photoperiod, Temperature and Water

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Abstract: The sharp increase in soybean (*Glycine max* (L.) Merrill) acreage in the late 20th century and early 21st century is due to the demand for edible oil and feed protein. However, a limiting factor in the extent of soybean cultivation is its high heat requirements and response to photoperiod. Most varieties are short-day plants and are generally the best-yielding genotypes. At higher latitudes (longer day length), there is a delay in the occurrence of subsequent developmental stages and problems with plant maturation before the onset of autumn frost. Global warming allows the cultivation range of warm-season species (including soya) to be shifted; however, periodic droughts and very high temperatures limit crop production. Adverse weather events result in a reduction in soybean seed yield of around 30%. Environmental stresses related to day length, high and low temperatures and water shortage or excess have the greatest impact on soybean yields, as we have no influence on them and can only, to a very limited extent, offset their negative effects. This paper reviews the recent world literature on how soybean responds to these stress factors. The results of our own research were also used.

Keywords: abiotic stress; legumes; light stress; photoperiod; soybean; thermal stress; water stress

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1. Introduction

Soybean (*Glycine max* (L.) Merr.) is an extremely important crop for the entire modern world, due to its wide use for feed, consumption and industrial purposes [1]. Soybean seeds contain 33 to 45% protein characterized by a favorable amino acid composition; 18 to 24% fat, half of which is unsaturated fatty acids; and only 5 to 8% crude fibre [2]. They are also a source of many valuable compounds such as vitamins, mineral salts and antioxidants [3,4]. Soybean provides about 29% of the world's supply of consumer vegetable oil and 71% of the world's supply of soybean meal [5]. Soybean oil is suitable for direct consumption but also for refining other vegetable fats. The fatty acid composition of soybean is genetically determined but can also be modified by the course of the weather or fertilization [6,7]. Soybean is also used in the pharmaceutical and chemical industries. It is an excellent source of bioactive peptides, which have health-promoting properties [8].

The cultivation of soybean, a species of the legume's family, has additional economic and ecological benefits due to the ability of the symbiotic bacteria *Bradyrhizobium japonicum* to assist in the biological fixation of nitrogen. The amount of symbiotically assimilated nitrogen depends on the genetic properties of the legume plant, its symbionts, as well as a number of environmental factors and agronomic treatments [9,10]. Bethlenfalvay et al. [11] report that soybean in symbiosis with *B. japonicum* can fix between 40 and 300 kg N ha^{-1} per year. As a result, it has a low mineral nitrogen requirement and its cultivation benefits the soil environment and increases the yield of successor crops such as cereals [12,13]. Soybean also improves the physical and chemical properties of the soil. Thanks to its strong, well-developed root system, it positively influences soil structure and fertility through root secretions that activate nutrient mobility and mineralization [2].

Due to its versatile use, soybean is at the forefront of the world's agricultural economy as a major oilseed crop. In terms of cultivated area, soybean ranks fourth in the world (after wheat, rice and maize) and first among legumes. In 2020, it was grown on 127 million hectares worldwide, with a production of 353.5 million tonnes [14]. The world's main soybean producers are Brazil, the USA and Argentina, which provide 82% of the global soybean seed production [15]. The world's soy was used for direct human food (20%), animal feed (76%) and industrial processes (4%) in 2018 [16]. In Europe, soybeans were grown on 5294 thousand ha in 2020, with a production of 10,627 thousand tonnes, representing only 3% of world production [14]. Between 2015 and 2019, the European Union imported an average of 14 million tonnes of soybeans and 18 million tonnes of soybean cake per year, 94% of which came from outside Europe [17]. Soy production in the EU27 + UK reached 2.7 million tonnes in 2020; the total used soy volume including net imports amounted to 30.3 million tonnes of soybean meal, 1.8 million tonnes of soybeans and 2.7 million tonnes of soybean oil. The average EU27 + UK citizen consumes an estimated 61 kg of soy per year. With 55 kg, the largest share of soy products is embedded in the consumption of animal products such as meat, dairy, eggs and farmed fish. The direct use of soybeans and soybean oil for food adds another 3.5 kg, while the consumption of soybean oil in industrial products (biodiesel) amounts to an estimated 2.3 kg per capita [18]. The high demand for vegetable protein in Europe is an important reason to expand the acreage under soybean cultivation on the European continent.

Soybean is a short-day (SD) crop with high temperature requirements [19–21], so obtaining a satisfactory yield under temperate climate conditions is difficult. The climatic conditions for soybean cultivation in central and northern Europe are similar to those in other so-called 'northern' countries, such as southern Canada. The limiting factors for cultivation are the specific photoperiod requirements of this species, as well as temperature and precipitation, mainly during germination and flowering [22]. Soybeans require a soil temperature of at least 8 °C and an adequate number of warm days with a base of 10 °C (GDD—growing degree days) for germination [23]. Soybean grown in Poland may be exposed to unfavorable thermal conditions in spring and summer, which are characterized by high frequency and variability in years. Spring frosts are particularly dangerous. Żarski et al. [24] showed a significant trend towards an increase in the number of days with moderate and severe late spring frosts (<-2 °C) and a delay of several days in the date of the last frost. On the other hand, however, a favorable significant trend was shown for a shift in the onset of the period when the soil reaches 8 °C at a depth of 5 cm (the date of soybean sowing), an increase in the average temperature and a prolongation of the growing season with suitable thermal conditions for soybean, which indicates the possibility of growing this species in Poland, as well as in other regions of central Europe with a similar climate [25].

Crop yield varies from year to year and is influenced by both internal and external (environmental) factors, including stresses. Stress factors can be divided into two groups: biotic (competition, allelopathy, pathogen invasion) and abiotic (high and low temperature, water deficit and excess, harmful radiation, salinity, pollution, pesticides and others). The action of stress factors can lead to reversible or irreversible disturbances in the functioning of the plant and the structures that build it. These disorders may consist in disturbances in plant growth and development and in metabolic processes taking place in the cell, as well as in changes in the physical–chemical properties of cell structures [26].

Stress conditions, particularly abiotic ones, cause disturbances at the cellular level as well as secondary stresses, e.g., formation of reactive oxygen species (ROS), cell membrane damage, protein denaturation or osmotic stress at the cellular level. During abiotic stress, the following sources of ROS occur: the signaling pathway in which ROS are produced for signaling by participating in the abiotic stress response signal transduction network and the metabolic pathway in which ROS are produced as a result of an imbalance in metabolic activity. It has been found that an increase in the level of ROS negatively affects the cell by oxidative damage to membranes (lipid peroxidation), RNA, DNA and proteins, which in turn leads to oxidative destruction of the cell (oxidative burst), as well as can cause cellular toxicity due to the accumulation of ROS metabolite products in the cell [27,28].

The response of plants to adverse abiotic conditions is linked to an intricate network involving defenses at the cellular, physiological and morphological defences [29]. Plant responses at the cellular level are based on the cuticle (external protection), desaturation of membrane lipids to remodeling the membrane, activation of non-enzymatic and enzymatic antioxidant systems as a defense against ROS, accumulation of osmolytes and induction of molecular chaperones according to cell demand [30].

The effect of their action is a reduction in vital processes and inhibition of plant growth, which consequently leads to a decrease in yield and deterioration in quality [31]. It was found that abiotic stresses negatively affect the yield of crops, contributing to yield losses of 50–70% [32]. Furthermore, under natural conditions, simultaneous effects of several stresses, called multistress, are often observed. For example, water scarcity is usually accompanied by high temperature, which exacerbates drought stress (DS) [33–35]. Therefore, it is extremely important to understand the reaction of the plant not only at the cellular level but also at the physiological and morphological level. In addition, studies of natural variation provide an understanding of the evolutionary processes that affect the response of plants to stress conditions. It was found that exploring the natural variation in stress response traits helps to identify the sources of genetic variation, which makes it possible to understand the coordinated regulation of these responses and, as a result, leads to improved agronomic crops [36].

Under temperate climate conditions, soybean is exposed, primarily, to thermal stress related to low temperatures, light stress related to the length of the day and night (photoperiod) and water stress related to soil water scarcity (periodic droughts).

The aim of this study is to discuss the response of common soybean to the more important abiotic stresses occurring under temperate climate conditions that affect seed yield and quality. The considerations are based on the results of our own and other authors' research available in the national and international literature.

2. Light Requirements

Solar radiation is a crucial environmental factor that determines the success of soybean. The response of plants of this species to the length of daylight exposure influences reproductive processes such as flowering initiation, flowering, fruiting and seed filling, determining the timing of the start and end of each of these developmental phases, as well as these rates of change within the plant [37]. Plants use light signals to determine the timing of key developmental transitions; blue light primarily triggers photosynthesis, which converts light energy into chemical energy stored as carbohydrates. In germinating seedlings, light activates photomorphogenesis, triggering the transition from heterotrophic to autotrophic growth [38–40]. Light inhibits hypocotyl growth, promotes cotyledon opening and activates the expression of light-regulated genes [41]. Plants use multiple photosensory receptors so they can detect a very broad spectrum of light, from UV-B to far red (280–750 nm). With these receptors, they can assess light quality, intensity and duration. The sensory photoreceptors involved in perceiving differences between full light and shade light, including red and far-red light-absorbing phytochromes (phyA and phyB), blue/ultraviolet UV-A light-absorbing cryptochromes (CRY1 and CRY2) and UV-B sensing photoreceptor (UVR8) [38,39,42,43]. Canopy light signals perceived by photosensory receptors modulate the extent of these responses [38]. Cotyledons/hypocotyls' exposure to light has a significant effect on the initiation of *Rhizobium* infection and the development of nodules on the primary root of soybean seedlings. The effect of light is a substantial inhibition of nodulation on the primary root. This inhibition is seen if the cotyledons/hypocotyls are first exposed to light prior to inoculation, while exposure of soybean cotyledons/hypocotyls to light after inoculation can considerably augment nodulation [44]. It was found that the amount of light is crucial for nodulation. In the dark inoculated legume plants develop significantly fewer nodules [44,45]. It was established that short-term darkness benefits nodulation and blue light hinders nodulation by two soybean TGACG-motif-binding factors (STF1 and STF2), which are *Papilionoideae*-specific transcription factors and divergent orthologs of Arabidopsis ELONGATED HYPOCOTYL 5 (HY5) [40], a bZIP transcription factor that regulates growth in response to light [41,46], which acts as a mobile signal to coordinate shoot and root growth in response to light [47,48]. Furthermore, light signals also promote soybean symbiotic root nodules formation. The blue light receptor GmCRY1s-STF1/2 module holds a key role in integrating darkness/blue light and nodulation signals, as seen in Figure 1 by Ji et al. [40]. The light-induced soybean TGACG-motif binding factor 3/4 (GmSTF3/4) and FLOWERING LOCUS T (GmFTs), which move from shoots to roots, interdependently encourage nodule organogenesis. Light-activated root growth as well as N uptake are mediated by HY5 translocated from shoot to root [45,47].

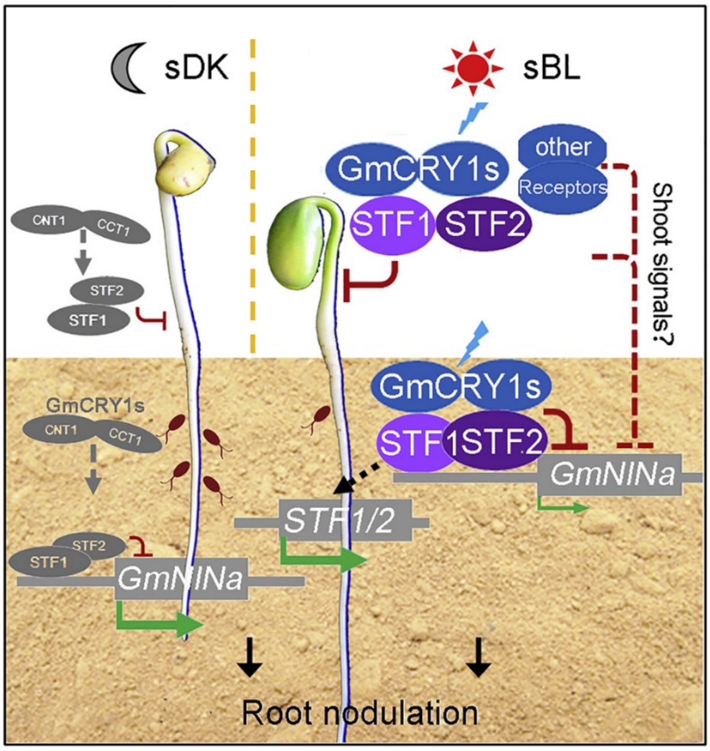

Figure 1. Light-dependent regulation of soybean nodulation from papilionoid-specific HY5 homologs.

Light also determines the course of developmental phases, modulates resource allocation and controls reproductive success. The strong effect of daylength on the flowering of soybean was demonstrated in early studies in the United States. At that time, Garner and Allard [49] classified soybean as a short-day (SD) plant and indicated the differential response of the four soybean cultivars when tested to the light induction period. As a SD plant in a temperate climate, soybean shows sensitivity to photo-thermal conditions while at flower set and development [50–53]. Its flowering as well as maturation time are regulated by genetic, environmental factors and their interaction [54]. Photoperiodism is a rhythmic change of sensitivity to light, which aids plants in regulating the flowering time according to seasonal changes in daylength and in adapting to growing conditions at various latitudes [55]. Gene × gene and gene × environment interactions have also been reported on flowering time [56]. Mathew et al. [57], under conditions of supplementary solar radiation during flowering and pod setting of soybeans, obtained increased yield, seeds, nodes, pods and number of branches per plant, pods per node and seeds per pod. In these authors' studies, light enrichment initiated at the late vegetative or early flowering stages raised seed yield 144 to 252%, primarily through increasing pod number, while light enrichment beginning at early pod formation enlarged seed size 8 to 23%, which led to a 32 to 115% enhancement in seed yield.

There is a delayed flowering barrier to higher soybean yields in the higher latitudes, where the light intensity (sun angle) is highest and the day length is longest early in the growing season, declining as the growing season progresses [37]. Flowering is usually inhibited under long daylight (LD) conditions but induced when the day length is less than the critical length [54]. It has been shown that under LD (16 h) conditions, the influence of the photoperiod on the thermal sensitivity is bigger under short daylight (SD, 12 h) conditions, whereas the impact of temperature on photoperiodic sensitivity is larger under low temperature (LT) conditions compared to high temperature (HT) conditions [52]. This trait heavily limits the cultivation area of a given soybean cultivar and effects the yield, plant architectures, and seed quality [51].

The sensitivity of soybean plants to photoperiod is one of the most relevant traits influencing the adaptation of individual soybean varieties to a particular location, with the appropriate varieties making the most of the growing season in the target region [49,58–60]. The sensitivity of soybean to photoperiod means that each genotype of this species is adapted to a narrow latitudinal zone [61,62]. Native to the 30~45° north latitude region of China, soybean is found in a wide range of latitudes and cultivated in broad regions, ranging from 50° N to 35° S latitude [63,64]. There are considerable differences in the photo-thermal response amid the different ecotypes. The yield of some soybean cultivars can be significantly reduced if they are grown at 2° N outside the normal growing latitudes [65]. Low-latitude (LL) ecotypes are more sensitive to the independent- and interactive-photo–thermal effects compared to high-latitude (HL) ecotypes [52,54]. For flowering induction, most cultivars of this species require a SD length. The high sensitivity of this species to photoperiod means that cultivation of individual cultivars is typically restricted to a narrow range of latitudes [54,64]. When soybean cultivars adapted to HL are sown in LL, they flower early, form low plants and develop few pods. Conversely, while cultivars adapted to LL are sown in areas of HL, they flower too late and usually cannot complete their life cycle before the onset of cold winter temperatures. Adaptation to SD conditions at lower latitudes involves delayed flowering, which prolongs vegetative growth for maximum yield potential [60]. However, the results of Seferova's [66] research on soybean genotypes in the conditions of the Leningrad region (59°71′ N, 30°41′ E) indicate that the response to day length and sunshine does not limit the range of soybean, so one of the leading breeding directions should be to reduce the plants' response to photoperiodism. In HL-adapted cultivars, the response of soybean plants to the photoperiod is weak or absent [54]. Plant adaptation to LD conditions at higher latitudes requires early flowering and a reduction or loss of photoperiod sensitivity [60]. Analyzing multi-year data (18 years), Cooper [37] showed that at HL (40° N), under the interaction of temperature and photoperiod, soybean begins flowering up to 2 weeks sooner than typical in reaction to above-normal temperatures in early spring. This leads it to enter the reproductive cycle sooner in the growing season, when days are longer and light intensity is higher, extending the reproductive cycle and increasing yield potential. In contrast, in the tropics, warm temperatures and short photoperiods strongly favor faster plant flowering and early maturity of light-sensitive varieties. Under such habitat conditions, the growing season is very short and seed yields are low [60].

Many plants use information about the changing length of day (photoperiod) to adapt flowering time to seasonal changes. The influence of the photoperiod on the time of flowering and the plants' maturity is a complex phenomenon. Many researchers have concentrated on the genetic and molecular basis of the HL adaptation of soybean. The wide adaptability of soybeans to different latitudes is due to genetic variation at major genes and quantitative trait loci (QTLs) that control flowering and maturity. Many naturally occurring variants at these loci were subject to human selection. This work has resulted in giving soybeans the flexibility needed to adapt to different areas and photoperiodic conditions. To date, 11 genes/loci (E1 to E11 and J) and several QTLs have been identified which control the time to flowering and maturity [60]. Dominant alleles in E1 [67], and two of its homologues E1La [55] and E1Lb [55,68]; E2 [68,69]; E3 [70,71]; E4 [72,73]; E7 [74]; E8 [62]; and E10 [75,76] inhibit plant flowering, while dominant alleles in E6 [77,78], E9 [79], E11 [80] and J [79,81–84] favor early flowering. Moreover, few QTLs, such as Tof11/Gp11 and Tof12/Gp1/qFT12-1 [82], Tof16 [85], LJ16.1 and LJ16.2 [86], are engaged in the control of flowering and maturity in soybean [60]. It was also shown that GmGBP1 functioned as a positive regulator upstream of GmFT2a and GmFT5a to activate the expression of GmFULc to encourage flowering under a SD condition [87].

The main maturity gene E1, a repressor of FLOWERING LOCUS T orthologs, has the greatest influence on flowering time and soybean sensitivity to sunlight [55,60,75]. According to Liu et al. [88], the greatest influence on latitude adaptation is exerted by the regulatory loci E1, E2, E3 and E4, which clarify about 60% of the molecular basis of soybean maturity. Mutations at four E loci gave rise to the diversity of flowering and maturity time, which were associated with the adaptation of soybean cultivars to diverse geographic regions and farming systems. It was shown that the flowering time and maturity of soybeans were significantly influenced by E1 and E2, especially E2.

A photoperiodic timing mechanism is present in leaves, and the main end effector of this pathway is the induction of the daylength-specific FLOWING LOCUS T (FT) gene, which encodes phlorigen [89]. A complete photoperiodic flowering pathway also has soybean cotyledons. The 'cotyledon-based self-reliance' model for soybean adaptation to high-latitude regions proposed by Xu et al. [90] is shown in Figure 2. Cotyledons perceive light and regulate the expression of GmFT2a as a flowering stimulus, which consequently initiates floral induction and facilitates the ecological adaptation of soybean plants to HL.

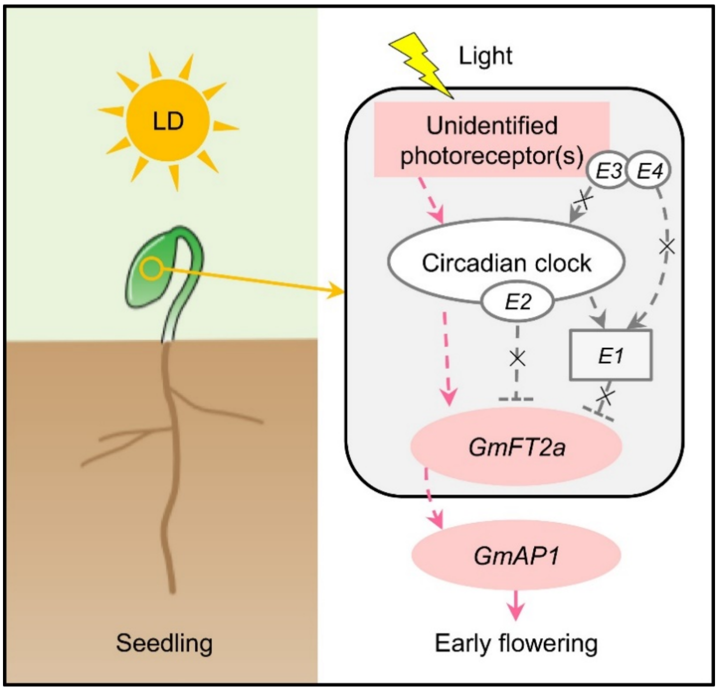

Figure 2. A cotyledon-based self-reliance model for flowering time regulation in early maturing soybean varieties. Orange arrow—gene regulation in the plant location framed by the circle; red and grey arrows—the promotion effect; T-shaped symbol—the inhibition effect; ×—the negation of inhibition.

It was shown that acclimatization to changes in photoperiod may be associated with changes in sucrose phosphate synthase activity in leaves. Huber et al. [91], under short photoperiod conditions (7 h), observed an increase in the rate of starch accumulation in soybean leaves, while the translocation rate, sucrose concentration and sucrose phosphate synthase activity decreased in relation to plants acclimated to LD conditions (15 h).

The light-sensitive locus has been shown to influence many agronomic traits in plants. In the case of beans, the photoperiod gene interacted with daylength to control the levels of the main physiological components of yield: the biomass, harvest index and days to maturity. The activity of photoperiod genes modulated by the length of the day also influenced the number of branches, nodes, leaves and leaf area as well as the rate of yield accumulation and sink activity [92]. In soybean plants, allelic variations in the loci governing the photoperiod sensitivity and growth habit produce a range of maturation precocity and have pleiotropic effects on grain yield and other agronomic traits, including plant height, lodging, seed weight and seed composition [62]. Under temperate climate conditions, as the sowing date is delayed (sowing seeds under conditions of lengthening daylight), the growing season of plants shortens [93]. The photoperiod controls the soybean's growth, which not only affects the flowering time but also the post-flowering vegetative and reproductive growth, such as the duration of pod filling, the development of the terminal inflorescence and the leaf senescence. According to Kantolic and Slafer [53] study, long photoperiods from flowering to maturity have been found to delay reproductive development in soybean and to increase the number of seeds per unit land area.

The photoperiod affects not only the induction of flowering but also the later stages of the reproductive growth of soybeans. The periods of flower differentiation, pod elongation and seed filling under SD conditions (9 h natural sunlight and 15 h darkness) are shorter than under extended day conditions (as for SD but with 3 h of low-intensity light in the middle of the dark period); furthermore, the seed's growth rate and the final seed's size are amplified by SD. It was shown that the number of growing seeds is improved under extended day conditions and decreases in SD, while SD increases seed growth rate and final seed size. The lack of differences in the final yield per plant between LD and SD was due to the mutual compensation of seed number and final average seed weight [94].

In addition to the photoperiodic response of soybean plants, the maturity group and the critical photoperiod can be indicators of plant sensitivity to light. Critical photoperiodis is defined as the dividing daylength between photoperiod sensitivity and photoperiod insensitivity phases and is one of the paramount indicators of photoperiod sensitivity [95]. Soybean varieties with different maturity groups may show different photoperiodic responses and, therefore, adapt to different daylength conditions and have different critical photoperiods. Yang et al. [59], examining 72 soybean genotypes belonging to 14 different maturity groups (MG 0000-MG X, based on the difference of 10 to 15 d of growth duration) [96] that were exposed to different photoperiods (12, 14, 16, 18 and 20 h day length), showed their significant variation in photoperiodic response. The critical photoperiod of the tested cultivars ranged from 16.4 h d^{-1} for MG 0000 to $\leq$12 h d^{-1} for MG IX to MG X.

For the course of photosynthesis and the maximization of the use of environmental resources, also important is the optimal plant density in the field. It can be crucial to reduce rivalry amongst plants for water, nutrients and light. Smaller plant density results in greater availability of light to plants, which results in less vulnerability to stress and promotes higher effectiveness of the soybean photosynthesis process. Jańczak-Pieniążek et al. [97] showed that the different row spacing and seeding density did not directly influence the productivity of soybean, proving the high phenotypic plasticity of soybean plants that depend on thermal and rainfall factors in a specific growing area. Sowing soybean in a smaller plant density, regardless of the row spacing, led to increased amounts of traits affecting the yield (number of pods and seeds per plant, seed weight) and the number and dry weight of nodules on the roots.

3. Thermal Stress

Low temperature (LT) stress is an environmental stress that limits plant growth and development processes [98]. In most species, LT adversely affects various physiological processes such as the following: the fluidity of membranes, nutrient and water absorption, the conformation of proteins and nucleic acids, alterations in cellular physiology through the decline in rate of metabolic processes or reframing of gene expression, free radical generation [99,100]. In soybean, cold stress has adverse effects primarily on protein and cell membrane metabolism [99].

Soybean is sensitive to the temperature throughout the growing season, i.e., from emergence to maturity, where a temperature range of 17–18 °C is considered the biological minimum and 22–32 °C the optimum, depending on latitude, cultivars tested and methods used [21,101–104]. A prolonged drop in the mean daily air temperature below 15 °C slows plant growth and inhibits leaf and shoot formation, while a drop below 10 °C disrupts the flowering process [20,105,106]. Soybean has lower heat requirements at maturity, which are at a biological minimum of 8–14 °C, with the optimum of 14–19 °C [21].

During the growing season of soybean, there are two critical periods related to the particular sensitivity of the plants to LT [21]. The first critical period is from sowing to full emergence. In order for plants to germinate well, soybean sowing should be done in soil warmed to 8–12 °C. LT cause delayed emergence and also, with high soil moisture, rotting of some seeds so that emergence is uneven and plant density may be unsatisfactory [107]. In a study by Staniak et al. [108], cold stress (12/6 °C day/night) prolonged germination and delayed emergence of 15 soybean cultivars; however, when the temperature was increased (20/15 °C day/night), the plants emerged quite quickly, and the plant density decreased by 9 and 4% on average, depending on the duration of stress (3 and 9 days, respectively). Other studies [109] confirm that if the completion of germination and the emergence of soybean seedlings takes place at higher temperatures (HT) (20 °C), the damage to seedlings caused by LT (5 °C) is low. Janas et al. [110] showed that cold stress at early developmental stages resulted in stunted shoot and root growth in soybean, with more reduction in root length than root mass (Table 1.). Cold stress in the rhizosphere layer also adversely affects the symbiosis of nodule bacteria with the legume, causing poor root nodules formation and lower amounts of nitrogen fixation. The effect of the stress is already apparent at the early stages of symbiosis. It inhibits the initiation of infection by reducing the bioactivity of the Nod factor [111,112].

Table 1. Effect of cold stress on length and dry weight of soybean root.

Number of Days with Chilling Stress	**Root Lenght (cm)**		**Dry Mass (mg·g^{-1})**	
	25 °C	**10 °C**	**25 °C**	**10 °C**
0	3.7 ± 0.4	3.7 ± 0.4	78.0 ± 7.0	78.0 ± 7.0
1	5.0 ± 0.4	3.9 ± 0.7	79.0 ± 6.0	76.5 ± 10.5
2	6.6 ± 3.3	4.0 ± 0.5	81.0 ± 8.0	79.5 ± 6.5
3	7.4 ± 0.4	4.1 ± 0.9	80.0 ± 10.2	79.0 ± 7.8
4	8.4 ± 1.8	4.1 ± 0.4	76.0 ± 5.6	79.5 ± 10.1

The response of the soybean to spring cold stress under temperate climate conditions would indicate the need for later sowing of soybean; however, numerous studies show that the LT during soybean sowing associated with earlier sowing significantly increases seed yield, compared to delayed sowing [108,113–117]. Soybean seed yield is positively correlated with the length of flowering, the pod setting and the seed-filling stage, so earlier sowing is beneficial in terms of the growing season length [118]. In a study by Staniak et al. [108] a 9-day cold stress applied after seed sowing (12/6 °C day/night), although delayed soybean emergence, increased plant vigor and positively influenced yields of 13 out of 16 soybean cultivars, which was associated with the development of a higher number and weight of pods and seeds per plant. According to Pedersen and Lauer [119], an earlier sowing date is associated with earlier flowering of the plants, which often avoids late summer drought and reduces disease and pest pressure. As a result, plants develop more pods and seeds per plant and, consequently, yield better. Late sowing of soybean accelerates emergence but also shortens plant vegetation due to the complex interaction of the temperature and photoperiod, which generally results in lower plants, fewer nodes, less vegetative mass at the beginning of seed filling and reduced flowering [118]. Late sowing is also generally associated with lower soil water resources, which can impair the seed germination and initial plant growth. Earlier sowing to avoid water stress is one strategy to counteract the adverse effects of climate change on crop production [120].

However, early sowing of soybean should be a prudent practice in colder regions due to late spring frosts [24]. Frost tolerance of soybean during the sowing period is relatively high, but it depends on temperature and seedling age [121]. At the germination stage (hypocotyl arch), the percentage of seedling survival at −6 °C is 75%, but at the fully developed cotyledon stage, already at −4 °C, the survival is 56% (Table 2) [122]. Thus, the later the frost, the greater the danger to the plantation, due to the more advanced plant development and the inferior stress resistance of older plants. On the other hand, it is also unfavorable to delay soybean sowing too much, due to the risk of prolonged vegetation and autumn frosts before harvest [122,123]. Late sowing is also associated with reduced soybean yields.

Table 2. Percentage survival of soybean seedlings as a function of temperature and seedling age.

Freezing Temperature (°C)	**Development Stage**			
	Hypocotyl Arch (1 Week after Planting)	**Fully Expanded Cotyledons (2 Weeks after Planting)**	**First Trifoliolate Emerged (3 Weeks after Planting)**	**Second Trifoliolate Emerged (4 Weeks after Planting)**
−2	100	94	94	87
−4	81	56	63	44
−6	75	19	0	13
−8	0	0	0	0

The second critical period of the particular sensitivity of soybean to cold occurs during the flowering phase [124,125]. The temperature course during the inflorescence formation period determines the number of flowers on the plant and the main shoot [126]. According to Gass et al. [21], the overcooling of plants at the reproductive stage can cause pod distortion or the formation of seedless pods, usually at the top of the stem, due to the failure of flowers to open during cold weather and the lack of pollination. Severe cold stress leads to flower drooping and limited or sometimes even no-pod setting, resulting in reduced yield and, in extreme cases, even no yield [107]. In a study by Ohnishi et al. [127], low temperatures (15/10 °C day/night) 3–4 days before soybean flowering adversely affected the fertilization process. The LT caused the formation of abnormal tetrad-shaped pollen grains, which significantly reduced pollination and, thus, the pod set and seed yield. In a study by Staniak et al. [124], a 7-day cold stress (17/13 °C day/night) at the flowering stage of soybean negatively affected plant structure and yield traits, causing significant reductions in the plant height (by 6.0%), node number (by 7.3%), stem dry weight (by 14.8%), number and weight of pods per plant (by 17.2 and 22.5%, respectively), number of seeds per pod and per plant (by 3.8 and 22.1%, respectively) and, consequently, seed yield (by 19.1%) compared to natural conditions (average 24/17 °C day/night) (Table 3). In contrast, Kurosaki and Yumoto [128] showed a significantly negative effect of a 2-week cold stress (18/13 °C day/night) at flowering on soybean generative organs (number of pods per plant), while there was little effect on vegetative organs (number of nodes, plant height). According to the authors, plant growth was almost complete at the flowering stage, hence the lack of statistically confirmed differences. Zheng et al. [129] report that soybean seed yield increased by 6–10% per 1 °C increase in mean daily temperature during the seed-filling phase, but the beneficial effect of temperature increases on yield depended on the basal temperature. This is supported by a study by Hatfield et al. [130] which showed that, in the southern states of the USA (mean temperature 26.7 °C), a 0.8 °C increase in temperature resulted in a 2.4% decrease in soybean seed yield, while in the central and eastern states (mean temperature 22.5 °C), the same temperature increase resulted in a 1.7% increase in yield.

Table 3. Plant and yield structure of soybean in relation to thermal conditions at flowering (average values for 16 cultivars).

Features	Natural Conditions (Average 24/17 °C)	7-Day Cold Stress (17/13 °C)	NIR (p = 0.05) Tukey Test
Plant height (cm)	79.6	74.8	2.57
Number of nodes	11.0	10.2	0.34
Stem dry mass (g)	5.35	4.56	0.51
Number of pods per plant	18.0	14.9	1.59
Weight of pods per plant (g)	12.0	9.3	0.96
Number of seeds per pod	2.36	2.27	0.055
Number of seeds per plant	41.7	32.5	3.13
Weight of seeds per plant (g)	8.17	6.61	0.66

Individual soybean cultivars may differ in their response to LT. Gass et al. [21] showed a variation in cold tolerance of 3 °C between 10 soybean genotypes. Other authors have demonstrated genotypic differences in pod-setting ability after LT exposure correlated with cold tolerance [25,131,132]. Cold-tolerant soybean genotypes can be distinguished at full maturity by assessing the regularity of pod distribution along the main shoot. Resistant genotypes have few or no sterile nodes after cold stress, whereas susceptible cultivars have a great deal of them [133]. In resistant genotypes, the good productivity of individual nodes is associated with reduced resting after stress and/or rapid levelling of damaged pods. In a study by Kurosaki and Yumoto [128], a cultivar that was more sensitive to post-cooling stress at the flowering stage had a significantly reduced number of pods per plant (by 64%), number of seeds per pod (by 28%) and 100-seed weight (by 44%) compared to the control, while a more tolerant cultivar had only a significantly reduced number of seeds per pod (by 13%) and a slightly reduced number of pods per plant (by 6%) and 100-seed weight (by 5%). According to Rahman et al. [134], in cool climates, soybean development from flowering to maturity is mainly controlled by temperature, as evidenced by the high regression coefficients (r^2 =0.88–0.95) obtained for the different cultivars. The breeding of cultivars with increased tolerance to abiotic stresses such as low and extreme temperatures is one of the most important tasks of soybean breeding in cold climates [127,135]. It is also one of the strategies to counteract the adverse effects of climate change on agricultural production [136].

The response of soybean cultivars to cold stress is also related to the maturity group. The International Soybean Seed Classification System [137] considers 13 maturity groups for soybean, classified from ‘000’ for very early cultivars to ‘X’ for very late cultivars. In Europe, commonly grown cultivars belong to maturity groups ‘000’ to ‘II’ [138]; in the USA, they range from ‘00’ to ‘IX’ [139]; in Brazil, from ‘V’ to ‘IX’ [140]; and in Argentina, from ‘II’ to ‘IX’ [141]. This is closely dependent on the latitude and climatic conditions of the regions concerned. The majority of commercial production is between 25° and 45° latitude and below 1000 m above sea level [142]. In the northern hemisphere, at HL, in the temperate climate zone (for example, Poland lies between the 49° and 54° parallels), early cultivars are usually sown. In a study by Staniak et al. [124], it was shown that under Polish conditions, later cultivars with a longer growing season ‘00’ reacted more strongly to cold stress (mean temperature 15 °C) at the reproductive stage and showed a higher yield loss than earlier cultivars (‘000’). Moreover, Kumagai and Sameshima [143] showed that an increase in temperature of only a few degrees in cooler climates (the average daytime temperature was 19.4–22.6 °C) significantly increased the seed yield of late-maturing soybean varieties, compared to the early varieties in which no such relationship was found. The different responses of soybean genotypes to thermal conditions during the flowering period may be due to different requirements regarding the length of the day and the growing season. In conditions of HT, a longer flowering period in late-maturing soybean varieties and a greater number of open flowers were observed, which in turn affect the increase in the number of pods and seeds and, thus, higher yields in these varieties compared to early-maturing varieties [53,144].

Plants have developed several strategies to deal with low-temperature stress, such as accumulating antioxidants and chaperones, activating the primary metabolism resulting in more energy production and altering the membrane structure which positively affects the osmotic balance of the cell [145,146]. It was found that the plants activate metabolic processes in their roots in cold stress conditions by increasing the amount of several metabolism-associated proteins, e.g., fructokinase, phosphogluconate dehydrogenase, NADP-specific isocitrate dehydrogenase, aconitate hydratase, glycine dehydrogenase [147]. Increased levels of proteins responsible for cell membrane permeability and signal transduction through the membrane have also been shown, e.g., annexins, prohibitins, stomatins, dehydrins. It is confirmed that abiotic stress associated with low temperature is responsible for oxidative damage to cells due to the formation of ROS and their precursors. Several antioxidants are produced in the roots in order to protect the plant from the destructive effects of ROS, e.g., oxalyl-CoA decarboxylase. In addition, high levels of scavengers ROS, produced by abiotic stress, have been found in plant roots, e.g., superoxide dismutase, ascorbic peroxidase and catalase [145]. Cold-related abiotic stress conditions promote the production of more heat shock proteins (HSP) in plant roots. These proteins act as molecular chaperones, facilitating the reformation of proteins as well as preventing the aggregation of denatured proteins [147]. Confirmation of the fact that defense-related pathways are activated in the root during cold stress control is the detection of defense-related proteins (e.g., disulfide isomerase protein) in the roots of peas grown under cold stress conditions [148].

Important regulatory proteins in cold tolerance have been found to form the CBF regulon, i.e., CBF1, CBF2 and CBF3 in *Arabidopsis* and wild tomato and additionally CBF4 and CBF5 in potato [149]. In turn, DREB1s/CBFs, e.g., DREB1A/CBF3, DREB1B/CBF1 and DREB1C/CBF2 in *Arabidopsis*, are important transcription regulators in the process of cold acclimatization of plants [150].

Thermal stress, defined as temperature fluctuations to more than optimal levels, can be associated with extremely high air temperatures, which can cause irreversible damage to the growth and development of the plant [151]. Heat stress is the cause of changes at the morphological, anatomical, metabolic and enzymatic levels. There is stunting of root and shoot growth, and sunburn may appear on the stem and leaves. As a result, there is senescence and abscission of leaves, and the productivity of plants decreases [152]. Soybeans tolerate HT well throughout the growing season, up to 32–38 °C [153,154], although some reports indicate that HT (up to 47 °C) do not cause significant damage to soybean plants [102,155]. However, very high temperatures at the flowering stage have been shown to cause cutting and dropping of flowers and young pods, resulting in a reduction in the number and weight of seeds per plant and, consequently, reducing plant yield [154,156,157]. Gibson and Mullen [153] showed that exposing soybean plants to temperatures of 35 °C for a period of 10 h during the day resulted in a 27% reduction in yield. According to Hossain et al. [151], plants exposed to temperature increases of 5 °C or more above the normal temperatures show repression in normal proteins and increased expression of a specific class of proteins called heat shock proteins or chaperone proteins, which contribute to heat tolerance. Heat stress also induces significant changes in fatty acid metabolism in soybeans, causing an increase in saturated fatty acids (oleic, stearic, palmitic) at the expense of unsaturated acids (linoleic and linolenic) [158]. According to Mustafa et al. [159] temperature fluctuation and DS affect the chemical composition of oil. Linoleic acid and linolenic acid are affected by warmer environments as their content decreases, while the oleic acid concentration increases. Temperature higher than 30 °C affects the activity of desaturase enzymes and decreases the sucrose level.

Soybean seeds can germinate at temperatures between 5 and 40 °C [160], but when subjected to prolonged exposure to HT, they lose germination strength. In a study by Dornbos and Muller [157], seeds that developed at 27/22 °C (day/night) showed 84% germination strength, while those exposed to a heat stress of 32/28 °C (day/night) for 35 and 60 days showed germination percentages of 73 and 56%, respectively. In other studies, conducted under controlled conditions, temperatures that reduced seed quality ranged from 33 to 38 °C [153,161,162]. Moreover, field studies have confirmed that HT during seed filling reduce soybean seed germination and vigor [163]. This means that the quality of the seeds reflects the integrated effect of the environment during seed production and the conditions to which the seeds were exposed during harvesting, conditioning and storage. The genotype of the soybean is also not negligible. Genetic variation among 44 soybean genotypes in response to HT (above 30 °C) was demonstrated by Salem et al. [164].

Heat shock transcription factors (HSFs) are responsible for regulating the expression of genes associated with heat tolerance. In the HSFs group, the central regulators are the HsfA1s responsible for the coordination of the downstream TFs and other signaling elements. HsfA1 has been shown to induce the expression of key TFs activating heat-responsive genes in *Arabidopsis*, i.e., HsfA2 and HsfA7a [165,166].

Thermal conditions significantly affect the chemical composition of soybean seeds [124,167–169]. Studies have shown that the fat content of soybean seeds is positively correlated with mean air temperature during the seed-filling phase [161]. In Howell's study (cited by Dornbos and Mullen [170]), as daily temperature increased (21.1, 25.0, 29.4 °C), oil content increased (to 19.5, 20.8, 23.2%, respectively), while protein content did not change. According to the authors, an air temperature between 20 and 40 days before full seed maturity has the greatest effect on oil content, as well as on fatty acid composition in soybeans. Moreover, in other studies, a decrease in oil content in soybean seeds was observed under LT conditions, with a concomitant increase in total protein content [170–175], and the opposite relationship was observed at higher temperatures [144]. In a study by Staniak et al. [124], a one-week overcooling of soybean at flowering (17/13 °C day/night) showed a significant decrease in soybean seed oil content (by 6.9%) and an increase in total protein content (by 4.1%) compared to natural conditions (24/17 °C). According to Kołodziej and Pisulewska [176], a 1 °C increase in minimum air temperature (13.4 °C) at the flowering stage of soybean resulted in an increase in oil yield by 7.7 kg ha^{-1}, while the same increase in mean daily temperature (19.9 °C) contributed to an increase in oil yield by 23.3 kg ha^{-1}, with the values of correlation coefficients at $r = 0.916$ and 0.922 and a significance level of $p = 0.01$. On the other hand, under heat stress conditions (35/20 °C day/night), an increase in protein content (by 4.0%) and a decrease in oil content (by 2.6%) in seeds were shown in the seed-filling phase compared to plants grown at lower temperatures (29/20 °C) [170]. A meta-analysis of environmental studies [177] showed a negative relationship between the protein and oil content in soybean seeds, which is also supported by other studies [178,179].

4. Water Stress

One of the environmental factors that can lead to disturbances in plant cell structure and function through biochemical and physiological changes is water stress—water deficit (drought) or water excess (flooding) [180]. In practice, it is far more common to encounter a soil water deficit, e.g., due to insufficient precipitation, than a water excess. In recent years, as a result of climate change, periodic precipitation deficits have become increasingly frequent in many European countries, including Poland, covering large areas and causing large losses in agricultural production [181]. According to Gerten and Rost [182], two-thirds of global food production takes place under water stress. In Poland, about 35% of arable land is permanently threatened by drought [183].

Restricted access to water causes water deficit in the tissues so that various physiological processes such as photosynthesis, transpiration and stomatal conductance are inhibited [184–186]. This affects plant growth and development and, consequently, determines seed yield and chemical composition [184]. Soybean has moderate water requirements and tolerates dry periods better than popular legumes, e.g., broad beans (*Vicia faba* L.), peas (*Pisum sativum* L.) or lupins (*Lupinus* sp.), grown under temperate conditions. It has genetic adaptations to do so, such as leaf and stem hairiness, which reduces excessive transpiration, and a deep, taproot system that allows it to draw water from deeper soil layers. In addition, soybean leaves, during times of high solar radiation, align themselves parallel to the incident sunlight (heliotropism phenomenon) so that the plant reduces the heating and the intensity of physiological processes.

Productivity loss under water deficit conditions depends on the phenological stage, duration and severity of the stress. In soybean cultivation, there are three critical periods associated with increased water requirements: the first period is from sowing to full emergence; the second at flowering; and the third at the pod-filling stage [2]. During germination, soybean seeds require a significant amount of moisture, accounting for about 120% of the seed weight [187]. Drought stress (DS) during this period causes similar effects as cold stress. A study by Michałek and Borowski [188] showed that under simulated drought conditions, a decrease in solution water potential significantly reduced the number of soybean seeds germinated, their germination rate and the sprout weight gain, and the drought affected seed germination more than young plant growth. Another study found that water deficit stress significantly reduced soybean seed vigor, percentage of germinated seeds, chlorophyll and carotenoid content of soybean seedlings and shoot length compared to optimum conditions [189]. In a study by Lamichhane et al. [120], the main causes of non-emergence were as follows: seedling mortality due to clods or soil surface crust, non-germination and seedling mortality due to drought.

Water deficiency at the vegetative stage adversely affects plant morphological traits, such as internode length, number of nodes, plant height, height of first pod set [190,191], but also reduces leaf area, shoot dry weight and root elongation [192]. Staniak et al. [191] showed that under soil water deficit conditions (30% field water capacity), the soybean cultivars were lower (by 25% on average) and had a lower set first pod (by 15% on average). Desclaux et al. [190] noted a drought-induced reduction in the number of nodes per plant, resulting in lower plants, and internodes that started to grow under stress conditions were shorter. Long-term soil water deficit stress adversely affects morphological traits but also yield structure elements, i.e., number of pods and seeds and, consequently, yield. A study by Borowska and Prusiński [193] showed that, with decreasing water availability, the average yield of soybean decreased linearly, probably due to a significant shortening of the vegetative and generative stages. In contrast, a study conducted under controlled conditions showed that reducing the soil water from 60 to 30% of the field water capacity for 8 weeks significantly reduced the average seed yield of two early (000) and one later (00) soybean cultivars (by 12.3%), while it did not affect the thousand-seed weight (TSW) [191].

The greatest water requirement of soybean occurs at the flowering and seed-filling stage, but the water deficit at the seed formation stage is the most critical period for plant productivity, as it determines the number of seeds per pod and the seed weight [176,194,195]. A study by Sionit and Kramer [196] showed that the greatest reduction in soybean seed yield followed stress at the early formation and pod-filling stage, compared to stress at flower induction and flowering as well as early pod formation, due to the greatest reduction in seed weight. Drought at the flowering stage causes flower rejection, but, as the flowering process takes a relatively long time (3–4 weeks), the plant compensates for the rejection of flowers and young pods formed at the lower part of the stem by forming new flowers and setting pods at the top of the stem. The level of compensation is gradually reduced with the end of flowering and completely ceases with the completion of the formation of flowers, which is in the mid-stage of grain formation. This is why the worst effects of drought are in the mid-stage of the formation of the pods to the mid-stage of grain formation [194]. According to the authors, soybean is, therefore, more sensitive to drought in the reproductive stages (seed development and maturation) than in the flowering and pod formation stages. In a study by de Souza [197], soil water deficiency lasting from the onset of seed filling to full maturity shortened the seed-filling period by 7 days, resulting in smaller seeds (by 32%) and lower yield (by 44%). In a study by Michałek and Borowski [198] a 10-day DS at the onset of flowering and at the seed-filling stage reduced the pod production per plant and TSW in seven soybean cultivars, which contributed to a decrease in yield, both under controlled (by 49.1% on average) and field conditions (by 19.8% on average). The significant effect of the developmental stage and the duration of stress on soybean seed yield was confirmed by Eck et al. [199]. Long-term stress inflicted on plants from the beginning of flowering to the end of the full pod development and from the beginning of seed development to the end of the growing season reduced soybean seed yield more (by 45 and 46%, respectively) than that inflicted at earlier, vegetative developmental stages. In contrast, a smaller yield reduction was recorded when the stress was short-lived and occurred from the beginning or full flowering to the initial pod development stage and initiated at the beginning of seed development and terminated at the full seed development stage (by 9–13 and 15%, respectively). Reduced biomass parameters under drought conditions are associated with reduced photosynthetic intensity, resulting in impaired biomass accumulation and the movement of assimilates to seeds [184]. According to Frieler et al. [200], alleviation of water deficit in the flowering and grain-filling stages of soybean results in improved photosynthetic efficiency, leading to higher biomass yields and favorable effects on plant productivity [201].

Drought in the summer months is often combined with high air temperatures, exacerbating water stress [35]. It generally leads to faster maturation of soybean and a shortened flowering and seed-filling stage. According to Kobraei and Shamsi [202], such adverse climatic conditions can reduce soybean seed yield by 24 to 54%. In a study by Dornbos and Mullen [157], yield reduction under DS at the seed-filling stage depended on stress intensity and air temperature. The weight and number of seeds produced by plants decreased linearly with increasing water stress and increasing temperature (27–29 °C—optimum, 33–35 °C—heat stress), and drought at an optimum temperature reduced seed number more than seed weight, while the opposite was true at high temperature. In a study by Ergo et al. [203], the combined stresses of drought (20% field water capacity FWC) and heat (>32 °C) during the seed-filling stage adversely affected photosynthesis and chlorophyll fluorescence indices, indicating damage to photosystem II. The interaction of the two stresses reduced seed assimilation and impaired the seed-filling metabolism, which contributed to a reduction in seed number and weight, resulting in a reduction in soybean yield.

DS is a major factor affecting symbiosis and leads to decreased nodule formation, reduced nodule size and N_2 fixation [204,205]. Korsak-Adamowicz et al. [206] found that soybean developed the fewest nodules in years when rainfall was below 20 mm during the flowering period. Moreover, other authors showed a decrease in the activity of symbiotic bacteria and a reduction in N_2-fixing capacity under DS conditions [195,205,207,208]. The authors explained this with a disturbance in nitrogenase activity, which can cause carbon deficiency and oxygen limitation leading to impaired plant growth and productivity. In contrast, Purcell et al. [209] state that water deficiency promotes the accumulation of N_2-fixation products in soybean shoots, resulting in reduced feedback in the N_2-fixation in roots.

The photosynthetic intensity, plant biochemical traits and yield of soybean under DS also depend on genotype [210–213]. According to Buezo et al. [214], certain high-yielding cultivars are able to cope with mild drought through various defense mechanisms, such as accumulating more xanthophyll and antioxidant resources or water sparing and investing in growth and productivity. It was shown that more drought-tolerant cultivars showed higher yield and WUE (water use efficiency) index under soil water deficit conditions than sensitive cultivars. The defensive strategies of some soybean cultivars also involved a shorter vegetation period and a faster transition to the reproductive stage, which was associated with a better allocation and partitioning of assimilates for seed development [214]. The selection of cultivars should be adapted to the agrometeorological conditions of the region and habitat so that they can exploit the maximum yield potential. According to Mandić et al. [194], cultivars with a shorter growing season are more suitable for cultivation in dry regions, while those with a longer growing season are recommended in regions with more favorable agrometeorological conditions.

Oil and protein are the most important nutrients in soybean seeds. They are synthesized and accumulated in the seeds during the pod-filling stage. Soil water deficiency affects the nutrient content of soybean seeds, especially during the flowering and seed development stage [159,215,216]. Michałek and Borowski [198] showed a decrease in crude fat content (by 13.8% on average) and a slight increase in total protein content (by 6.2%) in seeds of several soybean cultivars subjected to periodic drought. Weather patterns strongly modify the fatty acid profile of soybean seeds [6] and the nutritional value of the oil [7]. Moisture limitation resulted in an increase in saturated fatty acids at the expense of unsaturated fatty acids. It was observed that a wet and cool year promotes the accumulation of C16:0, C18:0, C18:3n6, C14:0, C16:1, sC20:0 and 20:1 acid in soybean seeds [6]. Dornbos and Mullen [170], under drought conditions, also showed an increase in protein content (4.4% on average) and a decrease in oil content (2.9%) in soybean seeds, with a linear change in these nutrient contents as DS increased, as measured by the accumulation of stress days. The results of Ghassemi-Golezani and Lotfi [217] also showed that with increasing water stress at reproductive stages protein percentage was increased but oil percentage was decreased. Grain yield and protein and oil amounts per grain and yields per unit area were also decreased as a consequence of water limitation. Other authors have also reported a strong influence of weather conditions on the chemical composition of soybean seeds. In cool and wet years, harvested seeds generally have lower total protein and higher oil content, compared to years with warmer and drier weather [218,219]. According to Vollmann et al. [220], unfavorable environmental conditions such as LT and high precipitation in the northern regions of Europe increase the oil content and decrease the protein content of soybean seeds due to inadequate nitrogen fixation. In contrast, Kumar et al. [221] showed a significant ($p \leq 0.01$) negative correlation between protein content and latitude and a significant ($p \leq 0.05$) positive correlation between oil content and latitude. The protein and oil content of soybean seeds also depends on the position of the pods on the stem [159]. A meta-analysis by Rotundo and Westigate [177] showed that water stress reduces protein and oil content in soybean seeds, with the authors pointing out that protein content additionally depends on temperature, so the results may sometimes be inconsistent. In the Du et al. [112] study, nitrogen content increased under DS, as well as proline and soluble sugar content in soybean leaves, which increased the osmotic regulation capacity of the plants. The authors also showed that, in drought conditions, soybean growth is regulated by the metabolism and distribution of nitrogen. Reduced nitrogen metabolism efficiency under drought conditions significantly correlated with soybean seed weight. Wijewardana et al. [216] showed that seed protein, raffinose, sucrose, stachyose, linoleic and palmitic acids, N, P, K and Ca decreased whereas stearic, oil, linolenic and oleic acids, Zn, Mg, Cu, Fe and B increased in response to the deterioration of soil moisture conditions. A negative correlation between the oil and protein content of soybean seeds has been shown. In turn, changes in the accumulation and partitioning of nutrients in soybean seeds observed under water stress conditions cause changes in the chemical composition of the seeds.

Suppression of the photosynthetic electron transport chain has been observed under drought conditions, which, in turn, affects the allocation of excess excitation energy towards increased ROS production. However, in proteomic studies on soybeans under drought stress, the induction of several ROS scavengers, i.e., dehydroascorbate reductase, dehydrin, quinine reductase, glutathione S-transferase and γ-glutamyl cysteine synthetase, was found [222–224].

The plant root stress response to drought is similar to the mechanisms found in damaged cells [145]. Under these stress conditions, pentatrico peptide repeat proteins (PPR), protease inhibitors (phloem serpin-1, Knotted1 (kn1) and defense-related proteins have been identified in soybean roots. This confirms that proteins associated with defense and proteins reported to regulate programmed cell death (PCD) are involved in the root response to drought stress [223].

The plant response to major stressors, including drought, is modified by natural variation in regulatory processes [36]. It has been shown that the natural genetic variation of the genes responsible for the plant stress response to drought occurs as an allelic variation in the previously described loci, as well as new loci [225,226]. Muthamilarasan et al. [227] confirmed that patterns of drought-responsive genes and allelic variation of transcription factors (TFs) are important for local adaptation and selection. [227] Natural populations provide a source of stable evolutionarily alternative alleles for the adaptation of domesticated lines. Relatives of wild crops, in addition to variability in the known loci, have made it possible to identify new loci that allow the desired characteristics of crops to be enhanced [225], as in the case of the identification in wild soybean of a new C2H2-zinc finger type TF, GsZFP1 [228].

A type of water stress is also excess water, or flooding. This is the phenomenon of water ponding on the soil surface of an arable field [229]. It is estimated that about 12% of arable land worldwide may be periodically inundated with water, leading to yield reductions of 20–33% [230]. Soil waterlogging can occur in irrigated regions or under conditions of very heavy rainfall, which is particularly detrimental on heavy and poorly drained soils [231]. Flood stress affects primarily the plant growth and development by disrupting the light interception and gas exchange, which depletes oxygen from the soil and causes the roots to switch from aerobic respiration to anaerobic fermentation. As a result, CO_2 and ethylene accumulate in the soil, resulting in reduced ATP synthesis in the root cells and adversely affecting many metabolic processes in the roots, e.g., reducing photosynthetic and aerobic respiration rates [232,233]. A study by Sullivan et al. [234] found a negative correlation between flood duration (1–3, 4–6, 6–8 days) and plant height, pod number and soybean yield. In contrast, no significant correlation was found between flooding duration and seed weight, oil and protein content in seeds. Linkemer et al. [235] showed that soybean is more sensitive to flooding stress at an earlier reproductive stage (R1—first flower) than at a later stage (R5—seed initiation). The authors report that the loss of seed yield in soybean due to waterlogging at the R5 stage was due to lower seed weight, while, at the R1 stage, it was due to fewer pods per reproductive node and fewer branches. On the other hand, excess water stress at the vegetative stages (emergence to R1) caused insufficient oxygen supply to the roots, resulting in a disruption of root growth and function, root nodules formation, nitrogen fixation, photosynthesis and stomatal conductance [236,237]. According to Board et al. [238], water-logging stress significantly reduces N levels in soybean leaves to deficient levels, and plants show typical deficiency symptoms of this nutrient (older leaves turn light green and then yellow, and plants dwarf). According to the authors, of the macronutrients and micronutrients studied (N, P, K, Ca, Mg, S, Mn, Zn), nitrogen is the most important in explaining soybean yield losses due to waterlogging. Genetic variation in response to flooding stress in soybean has also been shown [239].

Plants have introduced several changes in gene expression profiles and at the level of cellular proteins that allow acclimatization to difficult conditions associated with soil flooding. In the early response of plants to this type of stress, changes in the amount of proteins involved in primary metabolism, energy production or secondary metabolism, among others, were found in the roots. The induction of proteins involved in the primary metabolism of amino acids (aspartate aminotransferase), sugars and polysaccharides (β-glucosidase G4, UDP-glucose dehydrogenase and rhamnose synthase) and lipids (lipoxygenase) were affected [240,241]. In flood stress conditions, a decrease in the amount of enzymes of the phenol synthesis pathway in soybean plants was also noted, such as phenylalanine ammonia lyase, dihydroflavonol reductase, 6-deoxychalcone synthase, as well as proteins involved in secondary metabolism, for example, caffeic acid 3-O-methyltransferase, S-adenosylmethionine synthethase and dihydroflavonol reductase [241]. Reduced amounts of these enzymes under conditions of abiotic stress associated with soil flooding justifies the effect of inhibited pigmentation as a way of energy conservation [145].

An adverse change caused by soybean cultivation under flood stress is a decrease in the synthesis of the main component of the plant cell wall—rhamnose synthase [241]. The observed inhibition of cell wall synthesis is the effect of plants coping with these conditions by reducing energy consumption. However, limiting the hydrolysis of cell wall polysaccharides allows for the preservation of carbohydrate resources in the cell wall, which probably helps plants survive under soil flooding conditions [242].

Under these stressful conditions, scavenger ROS, such as ascorbic peroxidase, peroxidase and superoxide dismutase, have been shown to be reduced [243–245], as ROS production is clearly limited during the hypoxic state. In addition, an increase in the amount of proteins involved in the processes of proteolysis and the folding and storage of proteins was noted, which confirms their probable participation in the exclusion of inactive, damaged proteins.

Moreover, proteins related to disease/defense against pathogens and abiotic stresses (glycosylated polypeptides, α-amylase/subtilisin inhibitors and chitinases) were increased in plant roots during flood conditions [242]. The increased amount of these proteins in the root confirms that molecular processes such as protein folding and degradation are involved in plant adaptive responses toward unfavorable environmental conditions [145].

Regulators of stress conditions associated with flooding and low oxygen tolerance include group VII of the ethylene reactive factor (ERF) type TFs (ERF-VIIs) [246]. The main function of the SUB1A gene, belonging to ERF-VII and detected in submersible-tolerant rice, is to reduce amino acid metabolism, carbohydrate consumption and elongation growth through hormonal regulation [247,248].

In turn, Pucciariello and Perata [249] confirmed that NO and ROS molecules are associated with the reaction of plants to low O_2 levels (from signaling to metabolic rearrangement). The O_2 and NO levels can influence the group VII ERFs and, thus, determine the biological and developmental processes of plants. For example, the N-end rule pathway modulates seed germination [250,251], shoot and leaf development [252] and photomorphogenesis [253]. This confirms that physiological root hypoxia plays a role in controlling some biological processes by crosstalking with ROS and NO-dependent pathways. ROS and NO produced in roots under hypoxic conditions may play a role in destabilising group VII ERF, providing an additional level of control over the N-end pathway-dependent signaling. Modulation of ROS, NO and HRA1 (hypoxia response attenuator 1) can cause the survival mechanism in low O2 conditions to be modulated in different phases of hypoxia, which in turn affects the better adaptation of plants to fluctuations in O2 levels in flood conditions [249].

One of the main factors affecting the quality of soybean seeds is the weather conditions in the pre-harvest phase. Successive cycles of absorption and loss of water by seeds due to rainfall or daily changes in relative humidity, especially those associated with HT, cause physiological, physical and morpho-anatomical changes in seeds. Under such weather conditions, cell compaction and rupture may be observed in the seeds, mainly in the cell layers of the hourglass and parenchyma, which leads to forming intracellular spaces. Characteristic wrinkles on the coat surface often exhibit on weathered soybean seeds, as shown in Figure 3 by Pinheiro et al. [254]. The presence of weathering damage leads to a reduction in seed germination and vigor.

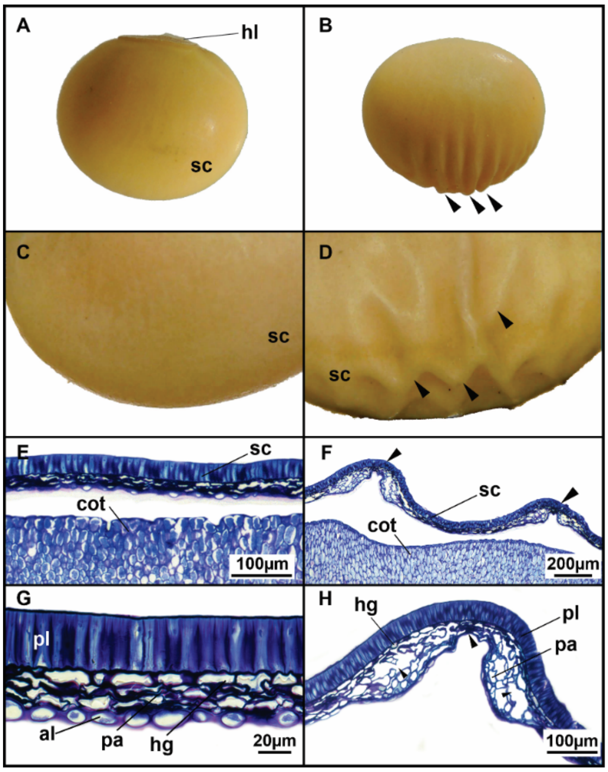

Figure 3. Morpho-anatomical characterization of soybean seeds with and without weathering damage. Overall perspective of the seed without weathering damage (**A**,**C**). Overall perspective of the seed with weathering damage (**B**,**D**). Anatomical section of seed without weathering damage (**E**,**G**). Anatomical section of seed with weathering damage (**F**,**H**). hl = hilum; sc = seed coat; cot = cotyledon; pl = palisade layer; hg = hourglass cells; pa = parenchyma tissue; al = aleurone layer. Arrows = seed coat wrinkling and cell rupture.

5. Summary

Climate change is strongly affecting crop productivity, as plants are exposed to various stress factors. In addition, the increasing demand for food from a growing world population requires significant improvements in agricultural productivity. Stress factors such as water shortage or excess or low or very high temperatures can disrupt the physiological processes of plants, affect their metabolism and damage cellular structures, resulting in stunted plant growth and contributing to reduced yield and impaired yield quality. Under abiotic stresses, reactive oxygen species (ROS) are released, which are by-products of altered aerobic metabolism. At high concentrations, ROS cause damage in cells, but at low and moderate concentrations, they act as secondary messengers in intracellular signalling cascades. Therefore, future research should be directed towards enhancing tolerance to stress factors by exploiting ROS-related pathways and identifying additional roles for ROS in plant acclimatization to abiotic stresses.

Photoperiod is a key factor that determines the range of soybean cultivation. Some soybean varieties, especially those grown in low latitudes, are not very sensitive to day length, which can be used in breeding work to improve the adaptability of soybean to different photothermal conditions. Using such genotypes as platforms, we can breed better and more adaptable soybean cultivars, thus, increasing the range of soybean cultivation.

An important direction for future research may also be to target better use of weather forecasts and to improve irrigation systems for soybean in cultivated fields. This will also allow the selection of cultivars showing optimal growth and yield under less favorable environmental conditions. Attention should also be paid to the problem of multistress, as, in agricultural practice, plants are often exposed to combinations of different abiotic stresses (e.g., high temperature and drought), which often have a stronger effect on plants than observed for the different stresses separately.

Knowing how plants react to stress factors and how they respond to stress is of great cognitive and practical importance. Numerous studies are testing ideas that can increase plant tolerance to abiotic stresses. The development of breeding programmes and innovations in agronomic practices can benefit soybean production in an era of climate change through the integration of knowledge and experience.

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