



Soybean Seed Responses to Defoliation Stress

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ABSTRACT

Background: Leaf loss (defoliation) is a common stress in soybean production, caused by both abiotic and biotic factors and it directly affects seed physiological and biochemical processes.

Methods: The experiment was conducted over two growing seasons (April 2024-November 2025). Defoliation was applied at the vegetative (V1) and reproductive (R1) stages at intensities of 33%, 67% and 100%. Seed quality was evaluated through standard germination tests, cold tests and analysis of lipid peroxidation and free proline levels.

Result: Partial defoliation during the vegetative stage improved germination and reduced the proportion of abnormal seedlings, whereas complete defoliation at flowering decreased seed weight, seedling vigor and cold tolerance. Elevated levels of lipid peroxidation and free proline indicated oxidative stress and activation of adaptive mechanisms. Both the intensity and timing of defoliation significantly influence seed quality and physiological resilience, providing valuable insights for the development of management strategies under mechanical and climatic stress conditions.

Key words: Defoliation, Seed quality, Soybean, Stress response.

INTRODUCTION

Soybean [*Glycine max* (L.) Merr.] is one of the most important leguminous crops worldwide, owing to its high seed protein and oil content, as well as its crucial role in sustainable agriculture through symbiotic nitrogen fixation (Sharma *et al.*, 2021). As a key resource for human nutrition, animal feed and industrial processing, soybean possesses exceptional economic and nutritional value (Mamlic *et al.*, 2025). Stable production and further advancement of the soybean industry rely on high quality seed, which transmits the genetic potential and adaptive mechanisms of the plant and thus represents the foundation of this research (Ebene *et al.*, 2020).

Seed quality plays a decisive role in ensuring stable yields and reliable production. Parameters such as germination, seedling vigor, physiological vitality, biochemical composition and thousand seed weight determine the success of the next crop generation and the long-term sustainability of the seed industry (Miladinov *et al.*, 2020). In the global context, seed production faces challenges posed by climate change, increasing food demand and market requirements for stable and high-quality seed (Nasir *et al.*, 2025). Therefore, studies focusing on factors that shape seed quality, including stress models such as defoliation, are of fundamental scientific importance and direct practical relevance (Poudel *et al.*, 2025).

Defoliation, *i.e.* the loss of leaf area, is one of the most common stress factors in soybean production. It may result from biotic agents (insects, pathogens) or abiotic damage (hail, mechanical stress), leading to reduced photosynthetic capacity and disruption of assimilate accumulation (Zhang *et al.*, 2024; Motaphale and Bhosle, 2016). Consequently, seed formation, morphology, physiology and biochemical processes are directly affected (Du *et al.*, 2020).

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The objective of this study was to determine how defoliation, applied at different developmental stages of soybean (V1-vegetative and R1-reproductive), acts as a stress model influencing seed quality and selected biochemical indicators. Cultivars were used as an experimental framework to assess variability in responses; however, the primary emphasis of the study was placed on understanding defoliation as a stress factor and its impact on physiological and biochemical processes in the seed.

MATERIALS AND METHODS

Location and climatic conditions

The experiment was conducted during the 2024 and 2025 growing seasons at the experimental field "Rimski šančevi" of the Institute of Field and Vegetable Crops, Novi Sad, Serbia (45°20'N, 19°51'E). The site is characterized by a temperate continental climate, with pronounced seasonal

variations in temperature and precipitation. Data on average monthly temperatures and rainfall for the April-September period are presented in Table 1, enabling interpretation of plant responses within the context of actual agroecological conditions during the experimental years.

Plant material and experimental design

The study was conducted using two soybean genotypes: Fortuna (early-maturing cultivar, maturity group 00, plant density 550,000 plants ha⁻¹) and Rubin (medium-late cultivar, maturity group II, plant density 400,000 plants ha⁻¹). Both genotypes exhibit high tolerance to lodging but differ in phenological traits and plant architecture, making them suitable for comparative evaluation under stress treatments. The experiment was arranged in a split-split plot design with three replications per treatment. Each plot measured 5 × 3 m (six rows), while the total experimental area covered 27 × 50 m. The crop was grown under rainfed conditions, following standard agronomic practices. No significant occurrence of pathogens or pests was recorded during the vegetation period.

Defoliation treatments

Simulated defoliation was applied at two developmental stages according to the classification of Fehr and Caviness (1977): the vegetative stage V1 (formation of the first trifoliate leaf) and the reproductive stage R1 (beginning of flowering). At each stage, three levels of leaf removal were imposed: 33% (central leaflet), 67% (lateral leaflets) and 100% (entire trifoliate leaf). The petiole was retained in all treatments to preserve nodal structure. Defoliation was performed manually using sterilized scissors in the morning hours under stable weather conditions to minimize variability in stress response. Simple leaves (unifoliate), which appear immediately after the cotyledons, were not included in the assessment of leaf area and were not removed, as they have limited photosynthetic activity and physiological relevance during the V1 and R1 stages (Mun *et al.*, 2021). The focus was exclusively on trifoliate leaves, which represent the dominant photosynthetic surface at the analyzed stages.

Seed quality assessment

Thousand seed weight (TSW) was determined after harvest on mature samples adjusted to a standard moisture

content of 14%, by weighing 1000 healthy seeds using an analytical balance. The standard germination test was conducted according to ISTA (2019) rules. Seeds were sown in sand and incubated for eight days at 25°C and 95% relative humidity. Germination energy (GE) was recorded after four days, while on the eighth day germination percentage (GP), abnormal seedlings (AT) and dead seeds (DS) were assessed. Biochemical analyses were performed on seedlings obtained from the standard test: lipid peroxidation (LP) was determined following the method of Placer *et al.* (1966) and free proline (FP) according to Bates *et al.* (1973). The cold test was carried out to evaluate seed performance under unfavorable conditions. Seeds were sown in sand and incubated for seven days at 10°C, followed by four days at 25°C. At the end of the test, germination percentage (C-GP), abnormal seedlings (C-AT) and dead seeds (C-DS) were determined. Biochemical parameters were analyzed only within the standard test, as the objective was to assess the physiological status of seedlings under optimal germination conditions, without the additional influence of low temperatures in the cold test that could induce secondary stress responses and complicate data interpretation.

Statistical analysis

Data were analyzed using two-factor ANOVA (factors: year and defoliation level), followed by Tukey's HSD test for mean comparison $p \leq 0.05$. Interaction effects were evaluated using the AMMI model, including AMMI1 biplot analysis, with GenStat software (VSN International, Hemel Hempstead, UK).

RESULTS AND DISCUSSION

Standard germination test

Analysis of the standard germination test (Table 2) revealed that the intensity and developmental stage of defoliation significantly affected thousand seed weight (TSW) and germination energy (GE). The most pronounced negative effect was observed in the R1 100% treatment, where complete defoliation at the flowering stage resulted in reduced TSW and GE, accompanied by an increased number of abnormal seedlings (AT). This indicates that complete defoliation during the reproductive stage limits

Table 1: Average monthly temperatures and precipitation during the growing season in the period from 2024 to 2025.

Month	Mean monthly temperature (°C)		Precipitation (mm)	
	2024	2025	2024	2025
April	9.6	10.9	55.1	54.5
May	16.0	19.2	62.9	17.9
June	23.3	24.0	23.9	43.6
July	25.5	25.1	114.4	13.8
August	22.2	24.6	46.4	104.0
September	19.9	16.8	16.4	159.0
Average/Sum	19.1	20.1	319.1	392.8

the accumulation of seed reserves and compromises seedling uniformity. In contrast, the R1 67% treatment exhibited an adaptive response—seeds showed higher GE and fewer AT, suggesting that partial defoliation can stimulate compensatory mechanisms and maintain seed vigor. The results indicate that the timing and intensity of defoliation directly affect the balance between the loss of photosynthetic potential and the plant's adaptive responses.

Biochemical parameters

The analysis of biochemical parameters further elucidated the physiological basis of these differences. Lipid peroxidation (LP), an indicator of oxidative membrane damage, was reduced in the V1 33% and R1 100% treatments, suggesting that moderate stress during the early vegetative stage activates antioxidant mechanisms, whereas complete defoliation at the flowering stage reduces metabolic activity due to limited resources. Free proline (FP), a well-known osmoprotectant, was lower in the V1 100% and R1 33% treatments, indicating limited osmoprotectant accumulation under metabolic stress. These results indicate that the stage and intensity of defoliation influence oxidative status and osmolyte metabolism, directly affecting seed vigor and quality.

Cold test

Results from the cold test confirmed the adaptive potential of seeds under stress. Partial defoliation during the vegetative stage (V1 33%) enhanced germination under unfavorable conditions (C-GP), indicating a priming effect—the activation of protective mechanisms that increase seed resistance. Complete defoliation at the flowering stage (R1 100%) reduced TSW and compromised germination, confirming that extreme stress during critical stages has long-term detrimental effects on seed quality.

The obtained results are consistent with previous studies showing that severe defoliation during reproductive stages reduces seed reserve accumulation and negatively affects seed quality, particularly when carbohydrate availability is limited (Parvej *et al.*, 2025). Seed physiological traits, including longevity and stress-related metabolites such as free proline and lipid peroxidation, are strongly influenced by seed maturation conditions (Miladinov *et al.*, 2021). In legumes, complex genetic and metabolic regulators interact with environmental stressors during seed development, determining seed longevity and quality (Wang *et al.*, 2021). Overall, the intensity and timing of defoliation are key factors determining seed quality and germination performance in soybean.

Interaction between defoliation and year

Analysis of the interaction between defoliation and year of production revealed a significant impact of climatic factors on soybean responses to leaf loss stress. During the two-year experiment (2024–2025), meteorological data (Table 1, Fig 1) showed marked differences in temperature and precipitation, which influenced both the growing conditions

Table 2: Analysis of variance (mean squares) for seed quality and physiological traits of soybean seedlings after defoliation treatments.

Factor/trait	TSW	GE	GP	AT	DS	LP	FP	C-GP	C-AT	C-DS
Year										
2024	164a	83.67a	90.81a	4.07b	5.12b	6.01b	3.04b	87.90a	7.14b	4.67b
2025	137.68b	78.50b	86.29b	5.83a	7.90a	8.13a	4.66a	80.21b	8.79a	11.00a
Cultivar										
Fortuna	154.82a	83.55a	90.55a	4.76a	4.69b	8.24a	4.39a	85.00a	9.05a	5.67b
Rubin	146.87b	78.62b	86.55b	5.14a	8.33a	5.91b	3.31b	83.12b	6.88b	10.00a
Treatment										
Control	153.44abc	80.33bc	88.58ab	5.25a	6.42a	7.94ab	4.21ab	81.92b	8.25a	9.67a
V1 33%	155.58ab	82.25ab	88.83ab	4.75ab	6.25a	5.98d	3.31bc	85.67a	7.58a	6.75a
V1 67%	159.92a	80.58abc	87.58b	5.50a	6.92a	7.22abc	4.12abc	84.25ab	8.42a	7.33a
V1 100%	154.60abc	81.50abc	88.83ab	5.17ab	6.00a	6.97bcd	3.23c	84.42ab	7.83a	7.75a
R1 33%	147.05c	80.67abc	88.08ab	4.83ab	7.08a	6.76bcd	3.23c	84.25ab	7.25a	6.75a
R1 67%	149.08bc	82.83a	89.50a	4.25b	6.25a	8.38a	4.82a	84.58ab	8.42a	7.00a
R1 100%	136.22d	79.42c	88.42ab	4.92ab	6.67a	6.26cd	4.03abc	83.33ab	8.00a	8.67a

Different letters within each column indicate significant differences among treatments (Tukey's HSD, $p \leq 0.05$). TSW: Thousand seed weight; GE: Germination energy; GP: Germination percentage; AT: Abnormal seedlings; DS: Dead seeds; LP: Lipid peroxidation; FP: Free proline; C-GP: Germination percentage-cold test; C-AT: Abnormal seedlings-cold test; C-DS: dead seeds-cold test.

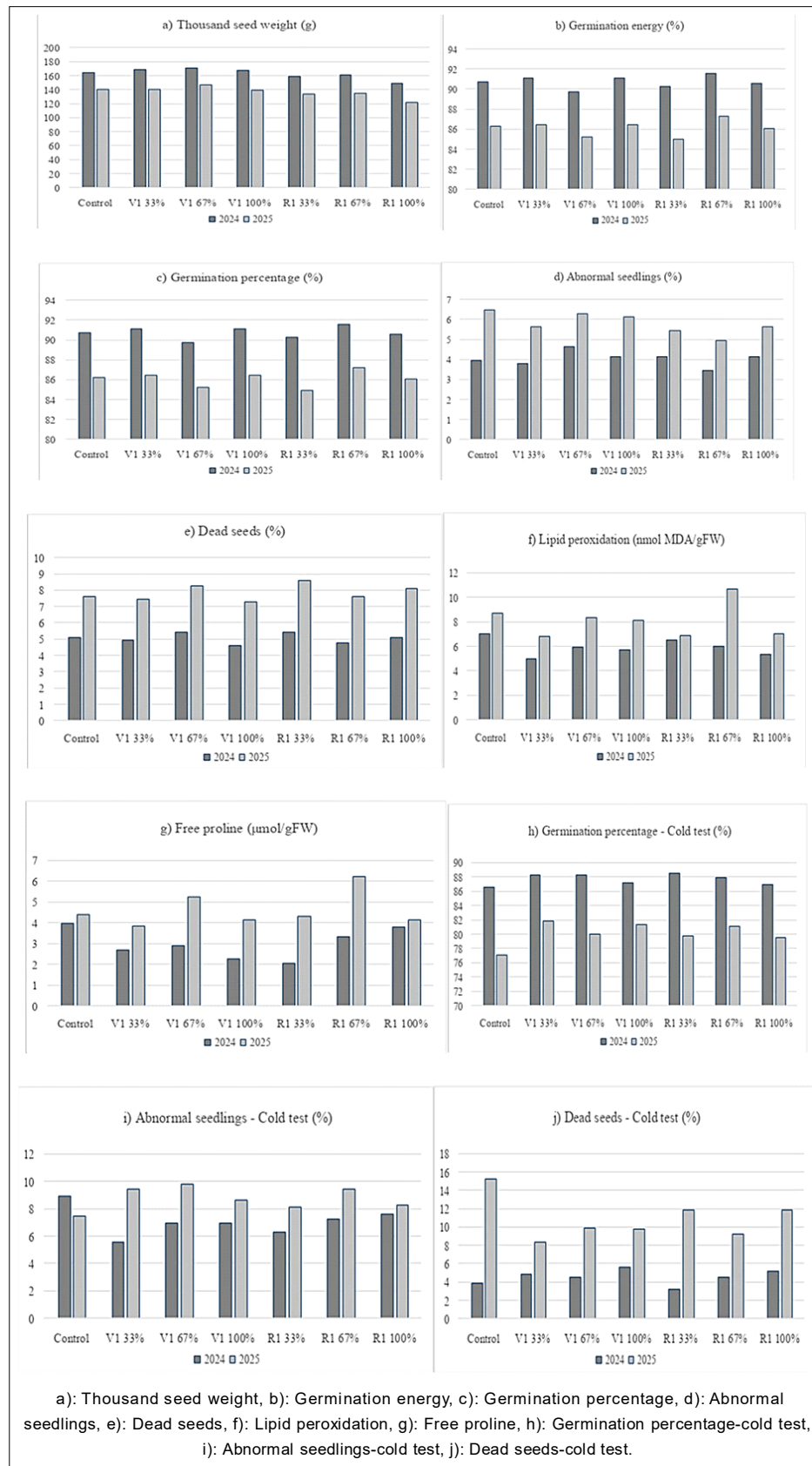


Fig 1: Interaction of defoliation treatments and year on seed quality and physiological traits of soybean seedlings ($p < 0.05$).

and the developmental dynamics of the plants. Under these conditions, the effects of defoliation were modulated by the interaction with climatic stress.

Standard germination test

Analysis of the standard germination test (Fig 1) demonstrated that germination values in 2024 were considerably higher across all defoliation treatments, likely due to more favorable and evenly distributed growing conditions. In contrast, the lowest GE and GP were recorded in 2025, particularly under complete defoliation at the flowering stage (R1 100%), highlighting the cumulative negative impact of defoliation combined with adverse climatic conditions during critical plant growth stages. A similar trend was observed for AT and DS, which showed increased values in 2025, especially under severe defoliation stress. These results suggest disturbances in seedling morphogenesis caused by intensified oxidative and osmotic stress resulting from unfavorable combinations of temperature and soil moisture.

Biochemical parameters

In 2025, elevated LP and FP values, particularly under 67% defoliation at R1, reflected enhanced oxidative stress and activation of osmoregulatory pathways, most likely representing an adaptive plant response to the combined stress of defoliation and unfavorable climatic conditions. Conversely, lower and more stable values of these parameters in 2024 indicate that plants experienced more adequate conditions to maintain physiological balance, even under defoliation stress.

Cold test

Cold test results further confirmed that seeds produced in 2024 exhibited greater tolerance to low temperatures, especially under mild defoliation (V1 33%), suggesting a possible “priming” effect, whereby moderate stress under favorable conditions stimulates protective mechanisms. In 2025, however, seeds showed reduced tolerance and increased sensitivity to cold stress, particularly under complete defoliation at flowering (R1 100%).

These findings confirm previous studies showing that the most sensitive stages of soybean seed development to defoliation-induced limitations of photoassimilates occur during early reproductive growth, leading to significant reductions in seed mass and quality (Poudel *et al.*, 2025). Seed longevity and physiological quality in legumes depend on complex intrinsic and extrinsic factors, including environmental stress during seed maturation, which directly affects germination potential and vigor (Ramtekey *et al.*, 2022). Osmoprotectants such as proline play a key role in mitigating abiotic stress by stabilizing cellular structures and maintaining osmotic balance, thereby enhancing plant stress resilience (Leonova *et al.*, 2024). Similar adaptive responses to moderate early-stage stress have been reported in other legumes, where controlled stress increases the accumulation of protective metabolites and improves seed performance under adverse conditions.

Interaction of defoliation and cultivar

The impact of defoliation on seed quality is often modulated by the genetic background of the cultivar (Fig 2). Different soybean cultivars may exhibit distinct physiological and biochemical responses to leaf loss, depending on their inherent tolerance mechanisms and growth characteristics. Therefore, evaluating cultivar-specific reactions to defoliation intensity is essential for understanding adaptive responses and optimizing seed production practices.

Standard germination test

Examination of germination parameters revealed cultivar-dependent responses. Only the R1 100% treatment caused a significant reduction in TSW in both Fortuna and Rubin, indicating that complete defoliation at flowering severely restricts seed reserve accumulation across genetic backgrounds. In Fortuna, defoliation did not significantly affect GE, whereas in Rubin, the V1 33% treatment increased GE, suggesting that partial vegetative defoliation may trigger adaptive mechanisms in this cultivar. No significant differences in GP were observed between treatments and controls in either cultivar. AT and DS also showed cultivar-specific patterns. In Fortuna, AT decreased under R1 33% and R1 66% treatments, whereas R1 100% increased DS. In Rubin, only the R1 100% treatment decreased DS, highlighting differential susceptibility of cultivars to severe defoliation.

Biochemical parameters

LP and FP responses varied between cultivars. In Fortuna, LP increased under V1 67% and R1 67% but decreased under V1 33% and R1 100%. In Rubin, all defoliation treatments lowered LP compared to the control. FP in Fortuna decreased under V1 33% and R1 100%, whereas in Rubin, it decreased under V1 100% and R1 33% but increased under R1 100%. These results indicate cultivar-specific activation of oxidative and osmoregulatory pathways in response to defoliation stress.

Cold test

C-GP increased in Fortuna under all defoliation treatments, while no significant effects were observed in Rubin. C-AT showed no significant differences between treatments and controls in either cultivar. In Fortuna, C-DS decreased under all treatments, whereas in Rubin, only R1 100% resulted in an increase. These findings suggest that cultivar identity influences the adaptive capacity of seeds under low-temperature stress following defoliation.

The results indicate that the genetic background of cultivars shapes their physiological and biochemical responses to defoliation. Differences in TSW and other performance traits under complete defoliation at flowering confirm that the developmental stage of stress critically affects reserve accumulation and subsequent seed performance. Variations in metabolites such as free proline and lipid peroxidation products reflect cultivar-specific regulation of oxidative and osmotic stress, which is key for

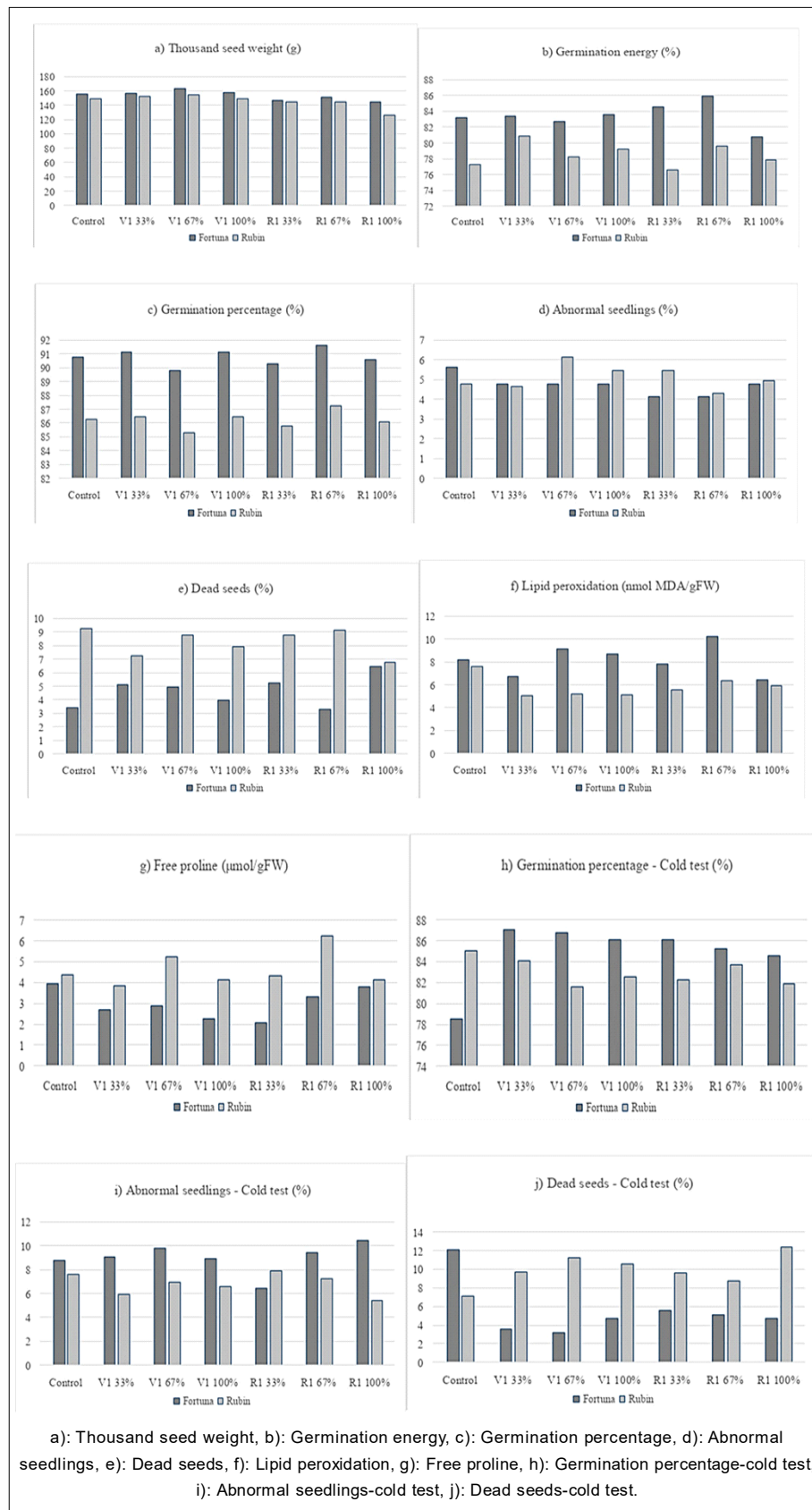


Fig 2: Interaction of defoliation treatments and cultivar on seed quality and physiological traits of soybean seedlings ($p < 0.05$).

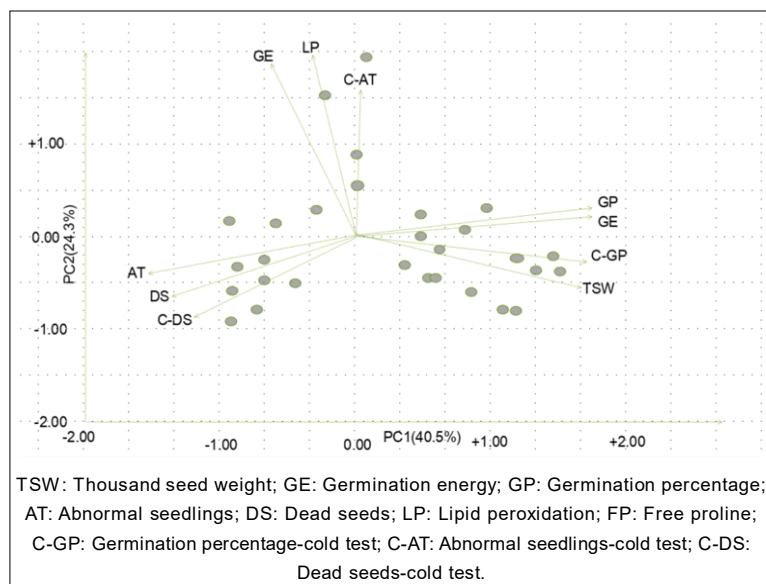


Fig 3: Multivariate analysis (PCA) of seed quality and physiological traits of soybean seedlings under defoliation stress.

maintaining seed vigor (Miladinov *et al.*, 2021). These findings highlight the importance of considering both cultivar genetics and defoliation timing in seed production strategies to preserve seed quality and enable adaptive physiological responses.

Multivariate analysis of physiological and biochemical seed traits

The PCA biplot illustrates the distribution of physiological and biochemical seed traits along the first two principal components, allowing evaluation of their interrelationships and collective response to defoliation stress (Fig 3). Traits associated with seed deterioration-AT, DS and C-DS-were grouped in the same direction, indicating strong positive correlations among these variables and their common involvement in seed quality degradation under stress conditions.

In contrast, traits related to seed vigor and germination-GP, GE, C-GP and TSW- were oriented in the opposite direction, revealing strong negative correlations with deterioration-related traits. This spatial separation confirms that increased occurrence of abnormal seedlings and dead seeds is directly associated with reduced seed vigor and germination performance.

Biochemical markers- FP, LP and C-AT- occupied an intermediate, orthogonal position relative to the deterioration and germination groups. This pattern suggests that these variables are partially independent of the main physiological axis of seed quality, reflecting specific stress-responsive biochemical and cold-sensitive processes. In particular, FP and LP appear to represent adaptive and oxidative stress responses to defoliation, while C-AT links stress exposure to impaired seedling development under suboptimal temperature conditions.

Overall, PCA separated seed traits into three distinct functional groups: (i) deterioration and loss of seed quality (AT, DS, C-DS), (ii) seed vigor and germination performance (GP, GE, C-GP, TSW) and (iii) stress-responsive biochemical and cold-sensitive indicators (FP, LP, C-AT). These findings confirm that defoliation acts as a stress factor that disrupts seed physiological stability while simultaneously activating biochemical response mechanisms that are not directly reflected in final germination outcomes.

CONCLUSION

Defoliation significantly affected soybean seed quality in a growth stage-dependent manner, influencing both physiological and biochemical traits. Partial defoliation during the early vegetative stage activated adaptive responses, resulting in improved germination performance, reduced occurrence of abnormal seedlings and maintenance of seed vigor. In contrast, complete defoliation at the flowering stage markedly reduced thousand seed weight, seedling vigor and stress tolerance, while increasing oxidative damage and indicators of osmotic imbalance.

The magnitude of these effects was further modulated by climatic conditions, with unfavorable weather intensifying the negative impact of defoliation. Although the study included two soybean cultivars, only minor differences in their responses were observed, without altering the overall interpretation of the results.

Overall, these findings highlight the critical role of defoliation intensity and timing, in interaction with environmental conditions, in determining seed physiological resilience and quality. The results provide practical guidance for optimizing soybean seed production and management strategies under increasingly variable climatic conditions.

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Disclaimers

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Conflict of interest

The authors declare that there are no conflicts of interest regarding the publication of this article. No funding or sponsorship influenced the design of the study, data collection, analysis, decision to publish, or preparation of the manuscript.

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