Article Type: Review Article

J Name: Modern Phytomorphology

Short name: MP

ISSN: ISSN 2226-3063/eISSN 2227-9555

Year: 2026

Volume: 20

Page numbers: 506-510

DOI: 10.5281/zenodo.19364216
(10.5281/zenodo.2025-20-506-510)

Short Title: Plant responses to defoliation under stress

REVIEW ARTICLE

Physiological mechanisms and recovery strategies of plant responses to defoliation under environmental stresses

Yufei Xie[1], Simiao Wang[1], Meng Zhang[1], Yirui Shao[3], Liyan Hou[3], Ning Wang[2], Xiao Liu[1*]

[1]School of Geography and Tourism, Qilu Normal University, Jinan, China

[2]School of Advanced Agricultural and Life Sciences, Weifang University, Weifang, China

[3]Shandong Provincial No.4 Institute of Geological and Mineral Survey, Weifang, China

[*]**Corresponding author:** Xiao Liu, School of Geography and Tourism, Qilu Normal University, Jinan 250200, China, Email: flippedlx@foxmail.com

Received: 02.03.2026, Manuscript No. mp-26-186107 | **Editor Assigned:** 04.03.2026, Pre-QC No. mp-26-186107 (PQ) | **Reviewed:** 18.03.2026, QC No. mp-26-186107 (Q) | **Revised:** 25.03.2026, Manuscript No. mp-26-186107 (R) | **Accepted:** 26.03.2026 | **Published:** 01.04.2026

Abstract

Defoliation caused by insect herbivory, anthropogenic disturbance, and grazing animals represents a significant challenge to plant survival and growth in forest ecosystems. This review synthesizes recent research findings on plant physiological responses to defoliation under various environmental stress conditions, including drought, low light availability, and varying plant sizes. Drawing from a series of experimental studies conducted on woody species, including *Robinia pseudoacacia*, *Amorpha fruticosa*, *Quercus acutissima*, and *Quercus rubra*, this review examines the complex interactions between defoliation and environmental factors. Key findings indicate that plants employ multiple compensatory mechanisms following defoliation, including enhanced photosynthetic rates in remaining leaves, mobilization of nonstructural carbohydrate reserves, and modifications in leaf morphological traits. The review reveals that environmental conditions significantly modulate plant recovery capacity, with drought and low light conditions generally suppressing compensatory growth responses. Furthermore, plant size emerges as a critical factor influencing recovery strategies, with larger seedlings demonstrating greater resilience through enhanced carbon reserve utilization. Native and alien species exhibit distinct response strategies, with native species investing more in chemical defenses while alien species prioritize growth recovery. These findings provide valuable insights for vegetation restoration practices and forest management strategies in the context of increasing climate variability and biotic disturbance pressures.

Keywords: Compensatory growth, Environmental stress, Forest management, Nonstructural carbohydrates, Plant recovery

Introduction

Plants in natural ecosystems are frequently subjected to leaf damage resulting from various biotic and abiotic disturbances, including insect herbivory, anthropogenic activities, and grazing animals. In the context of ongoing global climate change, the frequency and intensity of such disturbances are projected to increase, posing significant challenges to forest health and ecosystem stability. Defoliation, the removal of leaf tissue, represents one of the most common forms of biotic disturbance affecting woody plants, with profound implications for plant growth, survival, and ecosystem dynamics. Understanding the physiological mechanisms underlying plant responses to defoliation has therefore become increasingly important for predicting forest responses to environmental change and developing effective management strategies (Wang, et al. 2020, Javoy, et al. 2025).

Leaves serve as the primary organs for photosynthesis and carbon assimilation in most plants, making them critical for growth and survival. When leaf area is reduced through defoliation, plants experience an immediate decrease in their photosynthetic capacity, which can lead to carbon limitation and potentially threaten survival if recovery mechanisms are not effectively mobilized. However, plants have evolved a remarkable array of compensatory mechanisms that enable them to recover from defoliation events. These mechanisms include enhanced photosynthetic rates in remaining leaves, rapid production of new foliage, mobilization of stored carbohydrate reserves, and modifications in resource allocation patterns. The effectiveness of these compensatory responses can vary substantially depending on environmental conditions, plant species, and the timing and intensity of defoliation (Park, et al. 2024, Roitberg, et al. 2024).

Environmental factors such as water availability and light conditions play crucial roles in modulating plant responses to defoliation. Drought stress, which is becoming increasingly prevalent in many regions due to climate change, can significantly alter plant carbon balance and hydraulic function, potentially exacerbating the negative effects of defoliation. Similarly, light availability influences the capacity for photosynthetic compensation following leaf loss, with shaded conditions potentially limiting the plant's ability to generate the carbohydrates needed for recovery. The interaction between defoliation and these environmental stressors represents a critical area of research for understanding plant resilience in changing environments (Karami, et al. 2025, Gao, et al. 2026).

This review synthesizes findings from a series of our recent experimental studies examining plant responses to defoliation under various environmental conditions. The review focuses on woody species commonly used for vegetation restoration in warm temperate regions, including *Robinia pseudoacacia* L., *Amorpha fruticose* L., *Quercus acutissima Carruth*., and *Quercus rubra* L. By integrating findings across multiple studies, this review aims to provide a comprehensive understanding of the physiological mechanisms underlying plant recovery from defoliation and the factors that influence recovery success. The insights generated have important implications for forest management, vegetation restoration, and predicting ecosystem responses to environmental change.

Literature Review

Effects of defoliation on plant growth and carbon allocation

Defoliation significantly impacts plant growth and carbon allocation patterns, with effects that vary depending on the intensity and modality of leaf removal. Research on *A. fruticosa* and *R. pseudoacacia* seedlings has demonstrated that defoliation modality, specifically whether leaves are removed from the top down or bottom up, produces distinct effects on leaf traits and carbon allocation during the early recovery period. Studies have shown that plant growth in both species recovered after two months regardless of defoliation modality, suggesting the existence of effective compensatory mechanisms. However, carbon allocation patterns were significantly affected during the early recovery period, with full recovery occurring after approximately 60 days of treatment. The Nonstructural Carbohydrate (NSC) pool, comprising soluble sugars and starch, plays a crucial role in plant recovery following defoliation. When leaf area is reduced, plants rely on stored carbohydrates to support the production of new leaves and maintain metabolic functions. Experimental evidence indicates that defoliation leads to a rapid mobilization of starch reserves, which are converted to soluble sugars to compensate for reduced photosynthetic capacity. This mobilization is particularly evident in stem tissues, where starch concentrations decrease significantly following defoliation events. The soluble sugar to starch ratio serves as an important indicator of the plant's carbohydrate utilization strategy during recovery. Species-specific differences in recovery strategies have been documented, with *R. pseudoacacia* demonstrating faster recovery compared to *A. fruticosa*. Research has shown that NSC mass in *R. pseudoacacia* recovered to control levels within approximately 14 days following defoliation, while A. fruticosa required approximately 30 days for full recovery. This differential recovery capacity has important implications for species selection in vegetation restoration projects, particularly in areas prone to insect herbivory or other forms of defoliation. The faster recovery of *R. pseudoacacia* is attributed to more efficient compensatory physiological mechanisms, including enhanced photosynthetic rates and more rapid mobilization of carbon reserves (Wang, et al. 2020).

Interaction between defoliation and water availability

Water availability significantly modulates plant responses to defoliation, with drought conditions generally exacerbating the negative effects of leaf loss. Experimental studies examining the combined effects of low water availability and defoliation on woody Leguminosae species have revealed complex interactions between these stress factors. Under drought conditions, plants face simultaneous challenges of reduced water uptake and limited carbon assimilation, which can severely constrain recovery capacity. The interaction between water stress and defoliation is particularly relevant in the context of climate change, as many regions are experiencing increased frequency and severity of drought events. Research on *R. pseudoacacia* and *A. fruticosa* has demonstrated that plant size plays an important role in determining responses to combined drought and defoliation stress. Larger seedlings possess greater carbon reserves, which provide enhanced capacity for recovery following defoliation events. Studies have shown that large seedlings maintain more stable net assimilation rates under combined stress conditions compared to small seedlings, suggesting that carbon reserve availability is a key determinant of recovery success. The relative growth rate of total biomass was found to be significantly higher in small seedlings under favorable conditions, but this advantage diminished under stress conditions where carbon reserves became more critical. Hydraulic parameters, including stem-specific hydraulic conductivity and stem water potential, are significantly affected by both drought and defoliation treatments. Under drought conditions, defoliation can partially alleviate water stress by reducing the transpiring surface area, potentially improving the plant's water status. However, this benefit must be balanced against the loss of photosynthetic capacity. Studies on *Quercus* species have shown that native species such as *Q. acutissima* adopt a conservative 'slow strategy' under drought conditions, maintaining high hydraulic safety by reducing water potential and stem-specific hydraulic conductivity. In contrast, the alien *Q. rubra* maintains higher water transport capacity but is more susceptible to embolism under prolonged drought (Wang, et al. 2021, Wang, et al. 2023).

Defoliation under low light conditions

Light availability is a critical factor influencing plant capacity for compensatory growth following defoliation. Seedlings in regenerating forest layers are frequently attacked by herbivorous insects while growing under shaded conditions, making the interaction between light limitation and defoliation particularly relevant for understanding forest dynamics. Experimental studies have demonstrated that defoliation significantly suppresses plant growth under low light conditions, as the production of carbohydrates becomes insufficient to support recovery when photosynthetic capacity is limited by both leaf loss and light availability. Research on *R. pseudoacacia* and *A. fruticosa* has shown that compensatory growth in response to defoliation is more pronounced under high light conditions compared to low light conditions. Under high light availability, *R. pseudoacacia* seedlings recovered their total biomass within approximately 10 days following defoliation, while *A. fruticosa* required approximately 30 days for recovery. However, under low light conditions, both species experienced significant growth suppression, with recovery being substantially delayed or incomplete. These findings highlight the importance of considering light environment when predicting plant responses to defoliation in forest ecosystems. Leaf morphological and physiological traits exhibit sequential responses to combined light and defoliation treatments. Under low light conditions, plants typically increase specific leaf area and total chlorophyll concentration to maximize light capture efficiency. However, when defoliation occurs under these conditions, the plant's capacity to adjust leaf traits is constrained by limited carbon availability. Studies have shown that under low light conditions, defoliation first reduces growth parameters and specific leaf area, followed by reductions in gas exchange parameters and total NSC levels. This sequential response pattern reflects the progressive carbon limitation experienced by plants under combined stress conditions (Wang, et al. 2022).

Native *vs*. alien species responses to insect defoliation

The response strategies of native and alien plant species to insect defoliation differ significantly, reflecting evolutionary adaptations to local herbivore communities. Research comparing native *Quercus* species (*Q. acutissima*, *Q. aliena*, *Q. dentata*, *Q. variabilis*) with the alien *R. pseudoacacia* has revealed distinct patterns in secondary metabolite production and nutrient allocation following insect defoliation. Native species typically invest more resources in chemical defenses, producing higher concentrations of tannins, flavonoids, and total phenols following defoliation events. In contrast, alien species tend to prioritize growth recovery over defense investment. Following insect defoliation, native *Quercus* species significantly increased tannin and flavonoid concentrations compared to control treatments, while the alien *R. pseudoacacia* showed no significant changes in these secondary metabolites. This differential response reflects the 'enemy release hypothesis', which suggests that alien species may experience reduced herbivore pressure in their introduced range, allowing them to allocate fewer resources to defense and more to growth and reproduction. However, this strategy may become disadvantageous if herbivore populations increase in the introduced range. Nitrogen and phosphorus content in leaves also differed between native and alien species following defoliation. The alien *R. pseudoacacia* exhibited significantly higher nitrogen and phosphorus concentrations in defoliated plants compared to controls, suggesting enhanced nutrient uptake or allocation to support recovery. Higher leaf nitrogen content can boost photosynthetic capacity, potentially enabling faster recovery from defoliation. These findings indicate that alien species may possess advantages in recovery capacity, while native species invest more in resistance mechanisms. The tradeoffs between tolerance and resistance strategies have important implications for understanding plant community dynamics and invasion ecology. Discussion mechanisms of compensatory growth the research findings synthesized in this review reveal multiple mechanisms underlying compensatory growth following defoliation. The primary mechanisms include enhanced photosynthetic rates in remaining leaves, mobilization of stored carbohydrate reserves, and modifications in resource allocation patterns. These mechanisms operate in concert to enable plants to recover from leaf loss, with their relative importance varying depending on environmental conditions and plant characteristics. Understanding these mechanisms is essential for predicting plant responses to defoliation under changing environmental conditions. Enhanced photosynthesis in remaining leaves represents a rapid response mechanism that can partially compensate for lost photosynthetic capacity. Studies have documented significant increases in net photosynthetic rates following defoliation, particularly in the remaining leaves of defoliated plants. This compensatory photosynthesis is thought to result from increased nutrient availability per unit leaf area and reduced source-sink imbalances. However, the effectiveness of this mechanism is constrained by environmental factors, particularly light availability. Under shaded conditions, the capacity for photosynthetic compensation is limited by the fundamental constraint of light availability on photosynthesis. The mobilization of nonstructural carbohydrate reserves provides an alternative carbon source during the initial recovery period when photosynthetic capacity is limited. Starch stored in stems and roots is rapidly converted to soluble sugars and transported to support new leaf production. The size of these reserves, which varies with plant size and environmental history, determines the capacity for initial recovery. Larger seedlings with greater NSC reserves demonstrate enhanced resilience to defoliation, particularly under stressful conditions where photosynthetic recovery is constrained. This finding has important implications for seedling production and planting practices in restoration projects (Wang, et al. 2024).

Environmental modulation of recovery

Environmental conditions significantly modulate the effectiveness of compensatory mechanisms following defoliation. Drought stress and low light availability represent two major environmental constraints that can severely limit recovery capacity. Under drought conditions, plants face the dual challenge of maintaining hydraulic function while recovering from leaf loss. The interaction between drought and defoliation is complex, as defoliation can partially alleviate drought stress by reducing transpiring surface area, but this benefit must be balanced against the loss of photosynthetic capacity.

The research findings demonstrate that plant size is a critical factor determining recovery success under stressful conditions. Larger seedlings possess greater carbon reserves and more developed root systems, providing enhanced capacity for both carbohydrate mobilization and water uptake. This size-dependent resilience has important implications for restoration practices, suggesting that larger planting stock may be preferable in areas prone to defoliation or drought stress. However, the relationship between plant size and recovery capacity may vary among species and environmental contexts, warranting further investigation.

The differential responses of native and alien species to defoliation highlight the importance of evolutionary history in shaping plant defense and tolerance strategies. Native species, having coevolved with local herbivore communities, typically invest more in chemical defenses that deter herbivory. Alien species, released from their native herbivores, may allocate fewer resources to defense and more to growth. This 'enemy release' can contribute to the invasive success of alien species, but may also render them vulnerable if herbivore populations increase in their introduced range. Understanding these tradeoffs is essential for predicting the outcomes of species interactions in changing ecosystems.

Implications for forest management and restoration

The findings synthesized in this review have several important implications for forest management and vegetation restoration. First, species selection for restoration projects should consider not only growth rates and environmental tolerance but also recovery capacity following defoliation. *R. pseudoacacia*, despite being classified as an invasive species in some regions, demonstrates superior recovery capacity following defoliation, making it suitable for restoration in areas prone to insect herbivory. However, the potential ecological impacts of using alien species must be carefully evaluated in each context. Second, seedling size at planting can significantly influence establishment success, particularly in stressful environments. Larger seedlings with greater carbon reserves demonstrate enhanced resilience to combined defoliation and drought stress. While producing larger seedlings may increase initial costs, the improved survival and establishment rates may justify this investment, particularly in challenging restoration sites. Third, management practices should consider the interaction between defoliation and environmental stress. For example, thinning operations that increase light availability may enhance the capacity of understory seedlings to recover from herbivory.

Finally, the differential responses of native and alien species to defoliation have implications for managing invasive species and maintaining native biodiversity. Alien species that prioritize growth over defense may be particularly vulnerable to biological control agents that induce defoliation. Conversely, native species that invest heavily in defense may be more resilient to herbivore outbreaks but may also be slower to recover from other disturbances. Understanding these tradeoffs can inform integrated pest management strategies and conservation planning in forest ecosystems.

Conclusion

This review has synthesized recent research findings on plant responses to defoliation under various environmental stress conditions, revealing the complex interplay between biotic disturbance and environmental factors in shaping plant recovery. The key findings can be summarized as follows: (1) Plants employ multiple compensatory mechanisms following defoliation, including enhanced photosynthesis, carbohydrate reserve mobilization, and modifications in resource allocation. (2) Environmental conditions, particularly water availability and light, significantly modulate recovery capacity, with drought and low light conditions generally suppressing compensatory responses. (3) Plant size is a critical determinant of recovery success, with larger seedlings demonstrating enhanced resilience through greater carbon reserves; and Native and alien species exhibit distinct response strategies, with native species investing more in chemical defenses while alien species prioritize growth recovery.

These findings have important implications for understanding plant responses to environmental change and for developing effective forest management and restoration strategies. As climate change increases the frequency and intensity of both drought events and insect outbreaks, understanding the mechanisms underlying plant resilience becomes increasingly critical. Future research should focus on the long-term consequences of repeated defoliation events, the genetic basis of variation in recovery capacity, and the development of predictive models that can inform management decisions under changing environmental conditions. The integration of physiological understanding with ecological and evolutionary perspectives will be essential for predicting and managing forest responses to the complex challenges of the 21st century.

Funding

This work was supported by the Natural Science Foundation of Shandong Province (ZR2023QC238, ZR2023QC253), the Youth Innovation Team Science and Technology Support Project in Colleges and Universities of Shandong Province (2023KJ298), and the Fundamental Research Funds of Qilu Normal University (107002001365001).

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