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Short Title: Drought adaptation in *Quercus acutissima*

REVIEW ARTICLE

Drought adaptation mechanisms in *Quercus acutissima*: Physiological, hydraulic, and ecological strategies

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Abstract

Increasingly frequent drought events driven by climate change pose a significant threat to *Quercus acutissima*, a widely distributed species crucial for biodiversity conservation, soil stabilization, and plantation forestry in East Asia. Understanding its multidimensional adaptive mechanisms is essential for the sustainable management of this species in water-limited environments. This review synthesizes recent research across physiological, hydraulic, morphological, and ecological scales to comprehensively evaluate the response strategies of *Q. acutissima* to water deficit. Physiologically, the species exhibits pronounced overcompensatory recovery following drought and rewatering cycles and demonstrates a stress imprint effect, indicating ecological memory. Nitrogen and phosphorus addition effectively mitigates drought-induced reductions in the leaf structural traits, highlighting the role of nutrient management. Hydraulically, the species adopts a relatively risk-taking strategy characterized by a weak efficiency-safety tradeoff, but mitigates this risk through strong vulnerability segmentation, prioritizing the protection of main stems over expendable terminal organs. It also displays hydraulic lift and highly flexible seasonal water use, shifting between shallow and deep soil layers, which facilitates water complementarity in mixed plantations. Furthermore, the species is positioned at the fast investment-acquisition end of the leaf economics spectrum, exhibiting high phenotypic plasticity that favors rapid growth in resource-rich periods but increases its vulnerability under severe and prolonged drought. This vulnerability is further amplified by compound stressors, such as the synergistic negative effects of concurrent drought and defoliation, which severely deplete essential carbohydrate reserves. Ultimately, while these multiscale strategies explain their broad ecological amplitude, their acquisitive nature necessitates integrated silvicultural practices, such as optimized mixed species configurations and nutrient management, to reduce cumulative damage under climate extremes. Future research should prioritize long term field studies and belowground ecological dynamics.

Keywords: Defoliation, Hydraulic lift, Leaf economics spectrum, Overcompensation, Phenotypic, Plasticity, Vulnerability segmentation

Introduction

Quercus acutissima Carruth, a widely distributed species crucial for biodiversity conservation, soil stabilization, and plantation forestry in East Asia, plays a central role in natural forest ecosystems and commercial forestry. The species is valued for biodiversity conservation, soil stabilization, watershed protection, timber production, tannin extraction, and mushroom cultivation. In China, *Q. acutissima* has been widely planted for large scale afforestation and reforestation, especially in warm temperate and subtropical regions, serving as a key species for vegetation restoration on degraded lands and for cropland to forest programs. Its ability to thrive from lowland valleys to montane slopes reflects a broad ecological amplitude, making it an ideal candidate for ecological restoration and sustainable forestry (Liu, 2021).

Despite its ecological versatility and broad distribution, *Q. acutissima* faces mounting challenges from climate change. Rising temperatures, altered precipitation patterns, and increased frequency and intensity of drought pose serious threats to its survival, growth, and productivity. Drought, in particular, constrains photosynthesis, transpiration, nutrient uptake, and carbohydrate metabolism. The warm temperate zone in China, a region where *Q. acutissima* is widely planted, is characterized by arid and highly variable rainfall, deep loessial soils with low water holding capacity, and a long history of vegetation degradation. Understanding how *Q. acutissima* responds to water deficit is essential for predicting its future distribution, developing conservation strategies, and optimizing silvicultural practices under climate change (Hiejima, et al. 2025).

Recent research has elucidated drought adaptation mechanisms in *Q. acutissima* from leaf traits to whole plant hydraulic architecture and community level interactions. Studies have examined physiological responses to repeated drought and rewatering cycles, the mitigating effects of nutrient addition on drought damage, seasonal variation in water use strategies under different planting configurations, hydraulic efficiency-safety tradeoffs and vulnerability segmentation, positioning on the leaf economics spectrum and trait plasticity, and interactive effects of drought and defoliation. Several studies have compared *Q. acutissima* with co-occurring species such as *Robinia pseudoacacia* and *Q. rubra*, providing insights into relative performance and competitive dynamics in mixed communities.

This study synthesizes and integrates findings from these recent publications, with a focus on *Q. acutissima*. By comparing plant responses across experimental contexts and stress combinations, we identify common adaptive patterns, highlight knowledge gaps, and propose directions for future research. The review is organized into sections on drought and rewatering physiology, nutritional mitigation of drought stress, seasonal water use strategies, hydraulic architecture and vulnerability segmentation, leaf economics spectrum positioning and trait plasticity, and interactive effects of drought and defoliation. The ultimate goal is to provide a robust scientific basis for conservation, restoration, and sustainable management of *Q. acutissima* forests in an increasingly drought-prone world.

Literature Review

Physiological responses to drought and rewatering cycles

Drought is a major abiotic stressor that triggers a cascade of physiological and biochemical responses in woody plants. *Q. acutissima* exhibited pronounced overcompensation after rewatering: Photosynthetic rate, stomatal conductance, and transpiration rate not only recovered to pre-drought levels but frequently exceeded them. This overcompensatory response suggests robust physiological resilience and rapid recovery from intermittent water deficit, which is advantageous in environments with episodic drought. Mixed planting with *R. pseudoacacia* delayed the onset of drought symptoms in *Q. acutissima*, indicating that interspecific facilitation can enhance drought tolerance at the seedling stage. Importantly, hydraulic traits exhibited a stress imprint effect: Prior drought exposure altered subsequent hydraulic responses, potentially priming the species for improved performance under future drought. These results underscore the potential of planting configuration as a silvicultural tool to enhance seedling establishment and survival in drought-prone environments (Liu, et al. 2021).

Nutrient-mediated mitigation of drought stress

The interaction between nutrient availability and drought tolerance is a critical but often overlooked dimension of plant stress physiology. Liu, et al. (2024a) investigated how nitrogen and phosphorus addition affected the leaf structural traits of *Q. acutissima* seedlings under drought. Nutrient addition significantly alleviated drought-induced reductions in leaf area, leaf dry mass, and leaf volume, which otherwise constrain photosynthetic capacity and growth. Principal component analysis identified specific leaf area, leaf nitrogen concentration, and leaf dry matter content as key traits distinguishing treatment groups. The beneficial effects of nutrient addition were attributed to improved osmotic adjustment, higher photosynthetic enzyme activity, and enhanced cellular repair capacity. These results have practical implications: Targeted fertilization can improve the drought resilience of *Q. acutissima* plantations, especially on poor nutrient soils such as those in degraded landscapes.

Seasonal water use strategies and hydraulic architecture

Understanding how plants regulate water uptake and transport across seasonal gradients is fundamental for predicting responses to hydrological variability. Using stable isotope analysis, seasonal water use strategies of *Q. acutissima* and *R. pseudoacacia* were characterized under monoculture and mixed planting. *Q. acutissima* exhibited hydraulic lift, passively redistributing water from moist deep soil layers to drier upper layers *via* roots during periods of low transpiration. This behavior helps maintain root hydraulic conductivity in the upper soil and can facilitate water uptake by neighboring plants, particularly in mixed stands. Seasonally, *Q. acutissima* shifted its primary water source between shallow and deep soil layers in response to soil moisture availability: It relied more on shallow soil water during the growing season and switched to deeper sources in dry periods, reflecting a flexible and opportunistic water uptake strategy. In mixed plantings, the two species showed complementary water use, *R. pseudoacacia* primarily using shallow soil water and *Q. acutissima* accessing deeper layers, thereby reducing competition and enhancing stand level water use efficiency. These findings support mixed species plantations as a silvicultural approach to improve drought resilience in water-limited environments (Liu, et al. 2023).

Hydraulic efficiency-safety tradeoffs and vulnerability segmentation

Woody plant hydraulic architecture is governed by tradeoffs between efficiency and safety. This tradeoff was examined in *Q. acutissima* and three other woody species across seasonal gradients. *Q. acutissima* showed a weak efficiency-safety tradeoff, maintaining relatively high hydraulic conductivity without a proportional loss in cavitation resistance, a risk-taking hydraulic strategy that favors water transport under moderate water deficit but increases vulnerability during severe drought. Importantly, Q. acutissima exhibited strong vulnerability segmentation: terminal twigs were more vulnerable to cavitation than perennial shoots, protecting the main stem's critical hydraulic infrastructure. This segmentation allows the species to sacrifice expendable terminal organs while preserving primary vascular function, representing an effective drought survival mechanism. Seasonal dynamics revealed that Q. *acutissima* adjusted hydraulic conductivity and vulnerability to cavitation across the growing season, increasing efficiency when water was abundant and enhancing safety margins during dry periods (Liu, et al. 2020).

Leaf economics spectrum positioning and trait plasticity

The leaf economics spectrum describes a continuum from conservative to acquisitive strategies of resource allocation to leaf structure and function. Liu, et al. (2024b) quantified leaf economics spectrum positioning and trait plasticity of Q. acutissima and several other woody species along environmental gradients. *Q. acutissima* occupied the fast investment-acquisition end of the leaf economics spectrum, with high specific leaf area, elevated leaf nitrogen and phosphorus concentrations, and rapid photosynthesis and nutrient turnover. This acquisitive strategy enables the species to maximize resource capture and growth, consistent with its role as a pioneer successional species in disturbed habitats. *Q. acutissima* also showed high phenotypic plasticity across multiple leaf traits, indicating a strong capacity for environmentally driven trait modulation. Plasticity indices were greater than in more conservative species, suggesting that phenotypic plasticity is a key component of its ecological versatility. However, this strategy and associated plasticity may become maladaptive under severe and prolonged drought, where maintaining large, thin, high metabolic leaves incurs high transpirational costs and accelerates leaf senescence.

Interactive effects of drought and defoliation

In natural ecosystems, trees frequently experience multiple simultaneous stressors whose impacts interact. The combined effects of drought and defoliation on the physiological responses of *Q. acutissima* and *Q. rubra* seedlings were examined in our study. Defoliation significantly exacerbated drought-induced declines in photosynthetic capacity, stomatal conductance, and predawn leaf water potential in both species; the reductions were larger than those under drought alone. These interactive effects likely arose from the combined constraints of reduced leaf area and impaired water relations. *Q. acutissima* showed a somewhat greater capacity to recover from combined drought and defoliation stress than *Q. rubra*, indicating interspecific variation in tolerance to multiple stressors. Defoliation also depleted nonstructural carbohydrate reserves essential for drought recovery and basal metabolism. These findings highlight the need to consider multiple interacting stressors when assessing climate change vulnerability, as concurrent stresses may have additive or synergistic effects. Practically, pruning and thinning should be timed to avoid periods of water deficit to minimize compounded stress (Wang, et al. 2023).

Discussion

Synthesis of recent research reveals a multi-layered suite of adaptive strategies in *Q. acutissima*. Physiologically, the capacity for overcompensatory recovery after drought and rewatering cycles is particularly noteworthy. Rather than merely tolerating drought, *Q. acutissima* appears to invest actively in post stress recovery, potentially representing a bet-hedging strategy that maximizes growth during favorable periods while minimizing irreversible damage during drought. The stress-imprint effect in hydraulic traits indicates a form of ecological memory, where prior stress modifies subsequent responses; repeated exposure may either enhance resilience through acclimation or increase vulnerability *via* cumulative hydraulic damage under more frequent drought. Mixed planting with *R. pseudoacacia* delays drought onset, adding a community level buffer against water deficit (Liu, et al. 2021).

Hydraulically, *Q. acutissima* balances efficiency and safety in a manner tuned to its niche. The weak efficiency-safety tradeoff indicates a relatively risk-taking hydraulic strategy, maintaining high conductivity even under moderate deficit, which is complemented by strong vulnerability segmentation that protects main stems and perennial branches by sacrificing terminal organs (Liu, et al. 2021). Hydraulic lift further modifies rhizosphere hydrology, benefiting both the focal plant and neighbors; in mixed stands, it may act as a facilitative mechanism, although the net balance between facilitation and competition with *R. pseudoacacia* requires further study. Seasonal adjustment of hydraulic traits underscores dynamic regulation, with higher efficiency during well-watered periods and increased safety margins during dry periods (Liu, et al. 2023).

Positioning on the acquisitive end of the leaf economics spectrum integrates many observed leaf traits. High specific leaf area, elevated nutrient concentrations, and rapid turnover align with *Q. acutissima*'s role as a fast growing, early successional species in easily disturbed environments with rich resources. However, this strategy creates tension with drought tolerance: Large, metabolically active leaves increase transpiration and hydraulic risk. Nutrient addition can mitigate drought-induced reductions in the leaf structural traits, indicating that nutrient status modulates this tradeoff; well-nourished plants better maintain leaf function under deficit. High phenotypic plasticity in leaf economics spectrum traits further supports adaptive capacity under rapid environmental change (Liu, et al. 2024b).

The interaction between drought and defoliation highlights the complexity of natural stress regimes and the limits of single stressor studies. Recent syntheses on defoliation under stress have further elaborated that such interactions involve complex compensatory mechanisms that are strongly modulated by environmental conditions (Xie, et al. 2026). Defoliation amplifies drought-induced physiological decline, with important implications for forest health management where herbivory, pest outbreaks, or pruning coincide with drought. Pruning intensity and timing should be coordinated with seasonal water availability to avoid additive or synergistic stress. Interspecific variation in drought and defoliation tolerance between *Q. acutissima* and *Q. rubra* suggests that species selection for mixed plantations should consider tolerance to multiple concurrent stressors. Depletion of nonstructural carbohydrate reserves by defoliation is particularly concerning, as these buffers sustain metabolism during and after drought; practices that preserve nonstructural carbohydrate, such as avoiding heavy pruning during dry seasons and maintaining stand density to reduce individual tree water stress, may mitigate compound stress (Wang, et al. 2023).

From a broader ecological perspective, plant drought adaptation spans multiple scales. At the leaf scale, traits such as specific leaf area, nutrient content, and stomatal regulation balance carbon gain and water loss. At the whole plant scale, hydraulic architecture, vulnerability segmentation, and root distribution determine water uptake, transport, and survival under extreme deficit. At the community scale, planting configuration and interspecific interactions modulate water and nutrient availability, generating emergent properties not predictable from single species traits. Key knowledge gaps include the role of mycorrhizal associations in drought tolerance, long term acclimation of hydraulic and leaf traits under repeated stress, and belowground competitive dynamics in mixed plantations. Genomic and transcriptomic approaches could further elucidate molecular mechanisms underlying observed physiological responses and support breeding or selection of drought resilient *Q. acutissima* genotypes.

Conclusion

This study synthesizes the multidimensional adaptive strategies employed by *Q. acutissima* to navigate increasingly severe drought, framing its resilience across physiological, hydraulic, morphological, and ecological scales. Physiologically, *Q. acutissima* exhibits pronounced overcompensatory recovery following drought and rewatering cycles and demonstrates a stress imprint effect, indicating a robust ecological memory that primes the species for intermittent water deficits. Hydraulically, the species adopts a relatively risk-taking strategy characterized by a weak efficiency-safety tradeoff. However, this risk is effectively mitigated by strong vulnerability segmentation, strategically sacrificing expendable terminal organs to preserve the essential vascular function of main stems.

Furthermore, *Q. acutissima* is positioned at the fast investment-acquisition end of the leaf economics spectrum, exhibiting high phenotypic plasticity. This acquisitive strategy enables the species to maximize resource capture and rapid growth, explaining its broad ecological amplitude and role as an early successional pioneer. However, this same trait introduces an intrinsic vulnerability under severe and prolonged drought, as maintaining large, metabolically active leaves exacerbates water loss. Ecologically, its capacity for hydraulic lift and highly flexible seasonal water use, shifting between shallow and deep soil layers, facilitates water complementarity, particularly in mixed stands where pairing with species like *Robinia pseudoacacia* alleviates monoculture stress.

Despite these multiscale resilience mechanisms, the vulnerability of *Q. acutissima* is significantly amplified under compound stressors. The synergistic interaction between drought and defoliation severely depletes critical nonstructural carbohydrate reserves, hindering recovery and accelerating physiological decline. These insights highlight the limitations of single stressor studies and offer actionable directives for sustainable silvicultural practices. Effective management must transcend traditional approaches by integrating optimized mixed species configurations, targeted nutrient supplementation to maintain the leaf structural traits in degraded soils, and strictly timing pruning and thinning operations to avoid overlap with drought periods.

Looking ahead, while recent research has elucidated aboveground and individual level mechanisms, critical knowledge gaps remain. Future investigations must prioritize long term field studies to assess the consequences of cumulative stress imprints under increasingly frequent climate extremes. Additionally, exploring belowground ecological dynamics, specifically mycorrhizal networks and root competitive interactions, is essential for refining mixed stand designs. Finally, integrating genomic and transcriptomic approaches will unravel the molecular underpinnings of these adaptive strategies, facilitating the targeted breeding and selection of more drought resilient *Q. acutissima* genotypes for a drier future.

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