

Review

Adaptive Retention Silviculture During the Advancing and Killing Fronts of Beech Bark Disease

Lawrence Burns ^{1,*} , Heidi Frie ² and Nicholas LaBonte ³

¹ Division of Urban Forestry, Grand Haven, MI 49417, USA

² Michigan Department of Natural Resources, Lansing, MI 48933, USA; freih@michigan.gov

³ USDA Forest Service Eastern Regional Office, Milwaukee, WI 53202, USA; nicholas.labonte@usda.gov

* Correspondence: lburns@grandhaven.org; Tel.: +1-616-857-3493

Abstract

American beech remains a foundational late-successional species throughout eastern North America, yet Beech Bark Disease (BBD) continues to restructure northern hardwood forests across its range. This conceptual review synthesizes evidence supporting a framework centered on adaptive retention silviculture during the advancing and killing fronts of disease progression. Rather than arguing that thinning eradicates disease, the paper synthesizes historical and contemporary evidence suggesting that repeated selective thinning may function as a long-term ecological filtering process that preserves canopy continuity, reduces hazard accumulation, and favors vigorous and potentially resistant American beech phenotypes. The review integrates literature concerning stand density, disease ecology, aftermath forests, regeneration dynamics, biodiversity impacts, resistance forestry, and interactions with emerging Beech Leaf Disease (BLD). Collectively, the literature suggests that management actions during the advancing and killing fronts strongly influence future stand trajectories long before classical aftermath conditions emerge. Adaptive retention forestry is therefore interpreted as a resilience and persistence strategy rather than a disease-eradication framework.

Keywords: beech bark disease; American beech; adaptive retention silviculture; resistance forestry; aftermath forests; Beech Leaf Disease; northern hardwood forests; forest resilience

1. Introduction

American beech (*Fagus grandifolia*) forests across eastern North America, particularly within the northeastern United States and Great Lakes region, continue to experience ecological restructuring as beech bark disease (BBD) advances through susceptible stands. Although extensive research has examined the pathology and ecology of BBD, comparatively little synthesis has evaluated adaptive retention silviculture as a persistence-oriented management framework during the advancing and killing fronts of disease progression.

Existing literature remains dispersed across forest pathology, regeneration ecology, aftermath forest dynamics, resistance biology, and restoration forestry. This review synthesizes these complementary perspectives to evaluate how repeated selective management may influence forest resilience long before classical aftermath conditions emerge.

Recent advances in resistance breeding, propagation, long-term monitoring, and the emergence of Beech Leaf Disease have fundamentally altered the context in which Beech Bark Disease is understood and managed. Together, these developments provide an opportunity to reconsider adaptive retention silviculture within a broader framework



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emphasizing ecological persistence, conservation of naturally resistant genotypes, and long-term forest restoration.

American beech (*Fagus grandifolia*) remains one of the defining late-successional hardwood species of northeastern and Great Lakes forests. The species contributes substantially to wildlife forage, nutrient cycling, structural diversity, and canopy continuity [1]. Beechnuts provide critical mast resources for wildlife including black bears, small mammals, and birds [2]. These important ecological functions are increasingly threatened by an introduced disease complex that continues to restructure northern hardwood forests throughout eastern North America. Beech bark disease originated in Europe and was accidentally introduced into Nova Scotia during the late nineteenth century [3,4]. Since that time, the disease has spread gradually throughout eastern North America and into the Great Lakes region [5]. The disease complex involves interactions between the invasive scale insect *Cryptococcus fagisuga* and associated *Neonectria* fungi, particularly *Neonectria faginata* and *N. ditissima* [6]. Over time, repeated infection weakens canopy trees, contributes to radial growth decline, canopy dieback, windthrow, and eventual mortality [7]. Historically, management responses oscillated between passive acceptance and aggressive removal. More recent literature complicates both assumptions because infected trees frequently persist for decades and naturally resistant or tolerant phenotypes occur within affected populations [8,9].

For the purposes of this review, adaptive retention silviculture refers to repeated selective management intended to retain vigorous beech phenotypes, reduce structural deterioration, and influence future ecological trajectories while disease remains endemic within the forest.

2. Historical Understanding of BBD

Early understanding of BBD was shaped by the work of Ehrlich [3], who described a sequence beginning with infestation by *Cryptococcus fagisuga* followed by fungal colonization by *Neonectria* species. This model became foundational for later BBD management and research. The disease was eventually conceptualized as progressing through the advancing front, killing front, and aftermath forest stages [10]. During the advancing front, scale insects colonize previously uninfested stands. During the killing front, fungal infections intensify and mortality accelerates. The aftermath forest stage is characterized by altered stand composition, persistent diseased regeneration, and reduced mature beech abundance [10,11]. Subsequent research demonstrated that BBD produces cascading ecological effects involving reductions in wildlife forage, altered nutrient cycling, canopy restructuring, and broader biodiversity impacts [12].

2.1. Disease Ecology and Forest Dynamics

Contemporary research demonstrates that disease severity varies according to stand density, host age, bark chemistry, topography, and spatial clustering [13]. Dense beech stands create numerous potential introduction points for scale insects while simultaneously promoting humid microclimates favorable to disease development [14,15]. Larger trees additionally experience longer cumulative exposure periods and often possess bark conditions preferred by scale insects [16]. Together, these factors create substantial spatial heterogeneity within affected stands, reinforcing the need for adaptive management approaches that respond to local stand conditions rather than relying on uniform prescriptions. Importantly, disease expression does not necessarily result in immediate mortality. Coe et al. (2023) documented substantial radial growth reductions associated with BBD, yet infected trees frequently persist for decades despite chronic disease pressure [7]. This distinction changes the ecological meaning of management. If infected trees survive for extended periods

and some individuals exhibit tolerance or partial resistance, then management during the advancing and killing fronts may substantially influence subsequent stand trajectories.

2.2. *The Leak Framework and Long-Term Silviculture*

The long-term work of William Leak at the Bartlett Experimental Forest remains one of the most important silvicultural examples relevant to BBD management. Leak (2006) examined approximately fifty years of management directed toward removing poor-quality beech while retaining vigorous individuals within mixed northern hardwood stands [9]. His observations suggest that repeated selective thinning substantially reduced stand-level impacts of BBD on merchantability by favoring vigorous residual trees, reducing the accumulation of poor-quality, structurally compromised stems, and maintaining healthier long-term stand conditions despite continued disease pressure [9]. Leak did not claim that thinning eliminated disease. Instead, repeated stand entries appear to have shifted stand trajectories by favoring healthier, more vigorous, and potentially more resistant phenotypes. MacKenzie (2005) similarly reported that stands subjected to selective thinning experienced substantially lower subsequent mortality than unmanaged stands dominated by defective beech [17]. McLaughlin and Greifenhagen (2012) later concluded that gradual removal of diseased individuals combined with suppression of susceptible regeneration may represent one of the most effective long-term management strategies available [18]. Collectively, these studies suggest that management conducted during the advancing and killing fronts may influence the quality and composition of future beech populations even when disease remains present [9,17,18].

2.3. *Why Thinning Became Controversial*

Despite Leak's findings, thinning became increasingly controversial because disease dispersal itself is complex [9]. Cale et al. (2017) noted that disease incidence is not always directly associated with host density because scale insects may disperse long distances in air currents [6]. Researchers also observed that salvage cutting frequently failed to prevent dense beech regeneration and aftermath thicket formation [19]. Consequently, some managers interpreted these findings as evidence that thinning accelerated regeneration problems rather than improving forest conditions [19]. Much of the controversy, however, reflected differing management philosophies. Some approaches emphasized disease suppression itself, whereas others emphasized long-term stand resilience and persistence. These are not identical objectives. Adaptive retention forestry does not argue that thinning eradicates BBD. Instead, it proposes that selective thinning may improve the quality of persistence within diseased forests by influencing long-term stand structure and composition.

2.4. *Aftermath Forest Ecology*

The aftermath forest stage represents more than a static endpoint following disease-driven mortality. Cale (2014) proposed that the classic model of BBD development was overly simplistic and that multiple abiotic and biotic factors influence infection success in aftermath forests [20]. Bark phosphorus, bark chemistry, and interactions with the native scale insect *Xylococcus betulae* may significantly influence *Neonectria* infection dynamics [20]. Cale (2014) additionally demonstrated that dense beech thickets reduce floral diversity and alter understory structure [20]. These findings substantially expand understanding of aftermath forests beyond simple canopy mortality. Aftermath forests accumulate coarse woody debris, altered regeneration patterns, persistent disease interactions, and biodiversity impacts that may persist for decades after canopy mortality occurs. Collectively, these findings reinforce the central premise of adaptive retention silviculture: that management during the advancing and killing fronts can influence long-term stand

trajectories by shaping the ecological conditions that persist well beyond the initial wave of canopy mortality. Among the most consequential features of aftermath forests is the development of dense beech regeneration layers that can alter future stand composition and disease dynamics.

2.5. Beech Thickets and Regeneration Suppression

One of the most persistent ecological consequences of BBD involves development of dense beech regeneration layers following canopy disturbance. Root sprouting allows American beech to regenerate prolifically after injury or mortality [21]. Unfortunately, much of this regeneration remains susceptible to future disease development [11,19]. Giencke et al. (2014) demonstrated that aftermath forests frequently develop extensive beech thickets associated with altered stand dynamics and future disease persistence [19]. Zoller and McCullough (2022) documented increasing dominance of beech regeneration in affected Michigan forests while noting that dense beech recruits provide negligible wildlife habitat and suppress establishment of alternative species [22]. Dense beech thickets suppress the establishment of competing canopy species, reduce structural diversity, alter wildlife habitat quality, and perpetuate future disease susceptibility [19,22]. Within an adaptive retention framework, suppression of low-vigor beech thickets is not achieved through canopy thinning alone. Rather, declining beeches are selectively treated while vascular transport remains functional using approaches such as cut-stump or hack-and-squirt herbicide applications, thereby reducing subsequent root sprouting and shifting regeneration toward more desirable species over repeated management entries [23].

2.6. Resistance Forestry and Restoration

Contemporary understanding of BBD increasingly distinguishes between resistance and tolerance. Resistant trees exhibit reduced scale colonization or lower infection severity, whereas tolerant trees survive despite infestation and canker development. Houston and Houston (2000) demonstrated that resistant beech occur naturally within affected populations, while Koch et al. (2010) documented heritable resistance within American beech families [24,25]. Current restoration forestry increasingly focuses on long-term identification of vigorous survivors, scion collection, grafting, tissue culture propagation, and resistant-stock planting programs. Myers et al. (2023) emphasized the importance of integrating resistant-stock restoration pathways into long-term forest management [25]. Adaptive retention forestry therefore depends upon the assumption that naturally occurring variability within beech populations possesses long-term ecological value [24–26].

2.7. BLD and Compound Stressors

The emergence of Beech Leaf Disease introduces additional complexity into already stressed American beech systems. BLD typically begins with characteristic interveinal banding of newly emerged leaves. As disease severity progresses over successive growing seasons, canopy thinning, reduced vigor, branch dieback, and progressive tree decline become increasingly evident, thereby narrowing long-term management options for affected stands [27]. Although BLD differs biologically from BBD, the two diseases increasingly overlap geographically and ecologically [26]. Forest managers therefore face compound decline scenarios involving bark infection, foliar disease, regeneration bottlenecks, invasive species pressure that alters forest composition and regeneration dynamics, and climate-related stressors such as increasing temperatures, changing moisture regimes, and reduced seedling recruitment, all of which may further influence long-term forest resilience [28–30]. Loyd et al. (2024) explored therapeutic interventions involving fluopyram and thiabendazole for high-value trees and demonstration sites [27]. However, landscape-scale chemical treatment across extensive northern hardwood systems remains economically unrealistic.

The emergence of BLD therefore reinforces the importance of integrated adaptive management frameworks rather than disease-specific management approaches. Adaptive retention is therefore best viewed not as a treatment for BLD itself, but as a strategy for maintaining canopy vigor and ecological function despite the progressive physiological impairment associated with Beech Leaf Disease.

2.8. Implications for Great Lakes Forests

Great Lakes forests occupy an especially important position within contemporary BBD dynamics. They contain extensive northern hardwood ecosystems where American beech remains ecologically important and where managers increasingly confront overlapping challenges associated with BBD, BLD, recreation, and long-term stewardship. Northern hardwood systems associated with glacial moraines, dune complexes, and mesic hardwood landscapes often contain substantial beech components. These forests additionally support heavy recreational use, municipal park systems, wildlife habitat, and regional identity. McCullough et al. (2022) reported that 41% of beech trees across surveyed Michigan sites were dead by 2021–2022, with mortality concentrated among larger canopy trees [22].

Given these mortality levels, municipal forests and public park systems may face increasingly difficult management decisions [22]. As diseased trees continue to decline structurally, removal may become increasingly difficult, hazardous, and costly. Adaptive retention forestry provides an alternative framework emphasizing gradual intervention, retention of vigorous individuals, and proactive management before widespread structural decline occurs.

Consequently, one practical advantage of adaptive retention is that management can occur during the advancing front, before widespread structural deterioration characteristic of the killing front increases operational hazards, costs, and logistical complexity. Rather than reacting to extensive mortality, adaptive retention seeks to shape future stand trajectories through earlier, repeated intervention while management options remain safer, more flexible, and ecologically effective.

2.9. Adaptive Retention Forestry as a Persistence Strategy

Adaptive retention forestry should be interpreted as a persistence strategy rather than a cure-based framework. The objective is not elimination of BBD or BLD. Instead, the goal is maintenance of ecological function, structural diversity, wildlife value, and long-term resilience within diseased northern hardwood systems. Repeated selective thinning may function as a long-term ecological filtering process that preserves canopy continuity, reduces hazard accumulation, and retains vigorous phenotypes [9,17,18]. This perspective differs fundamentally from both sanitation forestry and passive acceptance of disease-driven stand decline. Forests may remain ecologically functional even when disease persists. Under this framework, success is measured not by disease eradication, but by maintenance of ecological function and long-term forest resilience. The central question, therefore, becomes whether management can improve the trajectory of persistence rather than eradicating disease entirely. A conceptual framework illustrating this persistence-oriented adaptive retention pathway is presented in Figure 1.

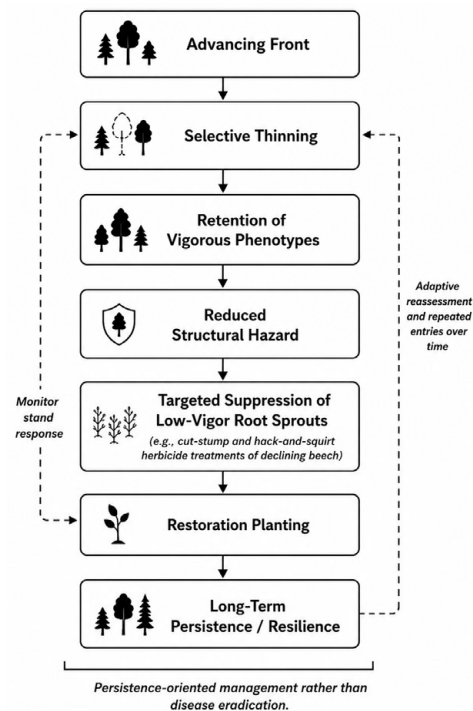


Figure 1. Conceptual framework proposed in this review illustrating adaptive retention during the advancing and killing fronts of beech bark disease (BBD). The schematic depicts a persistence-oriented silvicultural pathway in which repeated selective thinning and retention of vigorous phenotypes are intended to reduce structural hazard, suppress low-vigor beech regeneration through repeated monitoring and targeted suppression of susceptible beech regeneration while retaining vigorous phenotypes, and support long-term ecological resilience and restoration potential. The framework does not propose eradication of BBD, but rather emphasizes adaptive management aimed at maintaining canopy continuity, structural diversity, and functional persistence within diseased northern hardwood forests.

3. Conclusions

The scientific understanding of beech bark disease has evolved substantially during recent decades. Earlier assumptions that mortality was ecologically inevitable have increasingly given way to more complex interpretations involving stand structure, resistance, regeneration dynamics, and long-term ecological persistence. The literature reviewed here strongly suggests that adaptive retention silviculture deserves renewed consideration during the advancing and killing fronts of BBD. The work of William Leak remains especially important because it demonstrates that repeated selective thinning can influence long-term stand trajectories over approximately half a century [9]. Contemporary studies addressing aftermath forest dynamics, resistant-stock propagation, regeneration suppression, biodiversity impacts, and Beech Leaf Disease further reinforce the importance of integrated adaptive management systems [19,20,22,26,27]. The future of American beech in Great Lakes forests will likely depend upon strategic coexistence, restoration-oriented stewardship, repeated monitoring, and long planning horizons. Within this context, adaptive retention silviculture deserves renewed consideration as a persistence-oriented framework for sustaining ecological function while disease remains present.

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