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REVIEW

Mixedwood silviculture in North America: the science and art of managing for complex, multi-species temperate forests[1]

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Abstract: Temperate mixedwoods (hardwood–softwood mixtures) in central and eastern United States and Canada can be classified into two overarching categories: those with shade-tolerant softwoods maintained by light to moderate disturbances and those with shade-intolerant to mid-tolerant softwoods maintained by moderate to severe disturbances. The former includes red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill.), or eastern hemlock (*Tsuga canadensis* (L.) Carr.) in mixture with northern hardwood species; the latter includes pine (*Pinus*) – oak (*Quercus*) mixtures. Such forests have desirable socio-economic values, wildlife habitat potential, and (or) adaptive capacity, but management is challenging because one or more softwood species in each can be limited by depleted seed sources, narrow regeneration requirements, or poor competitive ability. Appropriate silvicultural systems vary among mixedwood compositions depending on shade tolerance and severity of disturbance associated with the limiting softwoods, site quality, and level of herbivory. Sustainability of mixedwood composition requires that stand structure and composition be managed at each entry to maintain vigorous trees of species with different growth rates and longevities and to encourage development of advance reproduction or seed-producing trees of desired species. Regardless of silvicultural system, maintaining seed sources of limiting softwoods, providing suitable germination substrates, and controlling competition are critical. Here, we describe commonalities among temperate mixedwoods in central and eastern North America and present a framework for managing them.

Key words: mixed-species forests, deciduous–coniferous mixtures, silvicultural systems, tree regeneration, shade tolerance.

Résumé : Les forêts mixtes (mélanges de feuillus et de résineux) tempérées du centre et de l'est des États-Unis et du Canada peuvent être classées en deux catégories principales : celles qui sont composées de résineux tolérants à l'ombre maintenus par des perturbations légères à modérées et celles qui sont composées de résineux intolérants et semi-tolérants à l'ombre maintenus par des perturbations modérées à sévères. La première catégorie comprend l'épinette rouge (*Picea rubens* Sarg.), le sapin baumier (*Abies balsamea* (L.) Mill.) ou la pruche du Canada (*Tsuga canadensis* (L.) Carr.) en mélange avec des espèces de feuillus nordiques; la deuxième catégorie comprend des mélanges de pins (*Pinus*) et de chênes (*Quercus*). Ces forêts possèdent une valeur socio-économique intéressante, un potentiel d'habitat faunique ou une capacité d'adaptation, mais leur aménagement est difficile parce que la présence d'au moins une espèce résineuse dans chaque catégorie peut être limitée par un manque de semences, des exigences de régénération trop strictes ou une faible capacité concurrentielle. Les systèmes sylvicoles qui sont appropriés varient en fonction de la composition de ces forêts et dépendent de la tolérance à l'ombre et de l'intensité des perturbations associées aux résineux critiques, à la qualité de la station et au degré d'herbivorie. La durabilité de la composition des forêts mixtes nécessite que la structure et la composition des peuplements soient aménagées à chaque rotation de façon à maintenir des arbres vigoureux d'espèces ayant des longévités et des taux de croissance différents et à favoriser le développement de la régénération préétablie ou d'arbres semenciers d'espèces désirées. Quel que soit le système sylvicole, il est essentiel de maintenir des sources de semences des résineux critiques, de créer des substrats de germination appropriés et de maîtriser la concurrence. Dans cet article, nous décrivons les points communs entre les forêts mixtes tempérées du centre et de l'est de l'Amérique du Nord et présentons une marche à suivre pour leur aménagement. [Traduit par la Rédaction]

Mots-clés : forêts mixtes, mélanges de feuillus et de conifères, systèmes sylvicoles, régénération des arbres, tolérance à l'ombre.

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Introduction

Silviculture must integrate knowledge of forest ecology, growth and yield, and operations while accounting for multiple goals depending on the context of application (Puettmann et al. 2009). The design of silvicultural systems is complicated by intricacies of stand structures and mixed-species compositions. Though challenging, mixed-species management is regarded as a means to maintain stand biodiversity and delivery of goods and ecosystem services, especially in a context of climate and economic uncertainty (Knoke et al. 2008; Jactel et al. 2017). In North America, mixedwoods are distinguished from other mixed-species forests by hardwood and softwood species in mixture, with neither component exceeding 75% to 80% of stocking based on basal area or canopy closure (MacDonald 1996; Canadian National Vegetation Classification, available from http://cnvc-cnvc.ca/index.cfm, 2013). Such mixtures often result from disturbances and stand developmental patterns that diversify ecological niches and accommodate tree species with different ecological requirements through complementary resource use (Coates and Burton 1997; Kneeshaw and Prévost 2007).

Mixedwood stands can be transient, as a result of natural succession or land-use legacies, or maintained through time by overlap of species distributions across latitudinal or altitudinal gradients (e.g., the temperate–boreal ecotone sensu Frelich et al. 2012) and disturbance regimes (Kneeshaw and Prévost 2007; Amos-Binks and MacLean 2016). Human-caused disturbances such as changes in fire regime or agricultural and forestry practices can alter the abundance and composition of forests (Namikawa and Kawai 1998; Boucher et al. 2009; Danneyrolles et al. 2019). Historical forest clearing and conversion to agriculture followed by agricultural abandonment, for example, ultimately led to development of eastern white pine (*Pinus strobus* L.) – oak (*Quercus* spp.) mixedwoods on many sites once dominated by late-successional hardwoods in central and southern New England (Whitney 1994). Throughout the region, preferential harvesting of softwoods is one of several factors contributing to a high proportion of hardwoods on previously softwood-dominated sites or increased hardwood dominance in mixedwood stands; this is implicated in widespread increases in species such as red maple (*Acer rubrum* L.) in central and eastern United States (US) and Canada (Fei and Steiner 2007) and various oak species in the Ozark Interior Highlands (Guyette and Dey 1997).

Mixedwoods can provide a number of ecological and commodity-production benefits, though these vary as a function of the composition and structure of stands and the health, vigor, and quality of individual trees (Comeau 1996; Kabrick et al. 2017). An oft-cited advantage of mixedwoods is the potential for increased productivity due to complementary resource use in stands of species with markedly different stature, structure, shade tolerance, or phenology (Kelty 1992; MacPherson et al. 2001; Brassard et al. 2011; Forrester 2014). In some cases, this can result in overyielding, a condition in which productivity of a mixture exceeds that expected based on compositional proportions alone (Pretzsch 2009; Waskiewicz et al. 2013; Lu et al. 2016). Furthermore, stands of mixed species confer market flexibility in the face of changing product demands and prices (Knoke et al. 2008). In the state of Maine, for example, pulpwood stumpage prices for spruce (*Picea* spp.) – balsam fir (*Abies balsamea* L. Mill.) (historically high) and hardwoods (historically low) reversed in the early 2000s (Maine Forest Service 2021). This resulted in loss of markets for landowners who had eliminated hardwoods from mixed stands in favor of softwood pulpwood production. Managing for mixedwoods provides some assurance that stands will retain value in the face of market fluctuations, particularly if management increases quality and vigor in addition to compositional diversity (Granstrom 2019). Moreover, managing for hardwood–softwood mixtures can help improve crop tree value, especially when hardwoods are stratified above softwoods that act as trainers, shading the lower bole to improve hardwood branch shedding and accumulation of knot-free wood (Prévost and Charette 2017; Puhlick et al. 2019).

Ecological benefits of mixedwoods include varied habitats to promote wildlife species diversity (e.g., Girard et al. 2004; Cavard et al. 2011; Fitzgerald et al. 2014; Martin and Raymond 2019), high functional diversity to maintain adaptability to stressors (Elmqvist et al. 2003), and decreased risk of damage by insect pests (e.g., Su et al. 1996; Zhang et al. 2018). From a forest health perspective, a number of studies suggest positive effects of hardwood–softwood mixtures on resistance to insect pests and diseases (MacLean and Clark 2021). Davidson et al. (2001), for example, reported that stand-level defoliation by European gypsy moth (*Lymantria dispar* L.) decreased as proportions of pitch, shortleaf, and Virginia pine (*Pinus rigida* Mill., *Pinus echinata* Mill., and *Pinus virginiana* Mill., respectively) increased in pine–oak stands. At the landscape scale, Campbell et al. (2008) observed that severity of growth reductions caused by spruce budworm (*Choristoneura fumiferana*) defoliation in spruce–fir stands decreased as hardwood content of the surrounding forest increased. Furthermore, work on forest carbon (C) suggests that mixedwood composition leads to increased carbon stocks in some species mixtures. This was observed for soil C in spruce–hardwood stands in New Hampshire (Jevon et al. 2019), though simulations of eastern hemlock (*Tsuga canadensis* (L.) Carr.) – spruce – hardwood stands in the same region suggested decreasing aboveground sequestration with increasing softwood proportion (Nunery and Keeton 2010). Yet, empirical studies based on long-term research plots found that increasing the softwood component of mixedwoods containing spruce–fir or eastern hemlock increased aboveground C stocks, though mixedwoods did not outperform pure softwood stands of those species (Kabrick et al. 2017). In the case of shortleaf pine in mixture with oak, increasing the proportion of softwoods is anticipated to have a positive effect on compatibility with future climate (Kabrick et al. 2017).

Despite benefits associated with some mixedwoods, composition can vary over time, transitioning toward either hardwood or softwood dominance following disturbance (Kern et al. 2021; Vickers et al. 2021). In particular, stands of hardwoods and softwoods in many temperate forests tend to move to a hardwood-dominated composition following repeated or heavy harvesting (e.g., Jensen and Kabrick 2008; Boucher et al. 2009; Rogers et al. 2018; Danneyrolles et al. 2019). Such changes also occur where the disturbance regime fails to provide a suitable substrate or light environment for establishing and recruiting the softwood component of mixedwood stands (Dovčiak et al. 2003; Olson et al. 2017). If a mixedwood composition is desired, managers must consider how to concurrently perpetuate hardwood and softwood species with different regeneration mechanisms, substrate preferences, light requirements, and growth rates when developing and implementing silvicultural systems. Typically, one or more softwood species within the mixture is challenging to regenerate with current management practices (e.g., Prévost et al. 2010; Pretzsch et al. 2015; Schweitzer et al. 2016; Raymond et al. 2018); we refer to these as limiting species.

Broadly, temperate mixedwood forests of central and eastern US and Canada can be classified into two overarching categories based on shade tolerance of limiting softwood species (Table 1). The first includes mixedwoods with softwoods of high shade tolerance that regenerate under low- to moderate-severity canopy disturbances. The second comprises mixedwoods with softwoods of low to intermediate shade tolerance that regenerate after moderate- to high-severity canopy disturbances, sometimes coupled with understory disturbance such as low-intensity fire. To support successful application of mixedwood silviculture in both categories, we present an assessment of the requirements of limiting species across five temperate mixedwood compositions in the US and Canada. Commonalities are identified and used as a framework for mixedwood management recommendations with broad application in temperate forests of central and eastern North America.

Table 1. Composition, limiting softwood species, natural disturbance regime, and regeneration ecology of selected temperate mixedwoods in two overarching categories based on shade tolerance of limiting softwoods.

	Mixedwoods with softwoods of high shade tolerance	Mixedwoods with softwoods of low to intermediate shade tolerance
Species composition	• Hemlock–hardwoods • Spruce–fir–hardwoods	• Eastern white pine – oak • Pitch pine – oak • Shortleaf pine – oak
Limiting softwood species	• Eastern hemlock • Red spruce • Northern white-cedar	• Eastern white pine • Pitch pine • Shortleaf pine
Disturbance regime in natural conditions	• Frequent small-scale and periodic moderate canopy disturbances	• Frequent surface fire or moderate to severe canopy disturbances
Regeneration	• Continuous to episodic	• Episodic
Competitive disadvantages of limiting species	• Reproduction primarily from seed (vs. vegetative) (though northern white-cedar frequently layers) • Small seeds require receptive seedbeds for germination and initial survival (e.g. decayed deadwood, mineral soil) • Slow growth relative to hardwoods (particularly sprouts) and balsam fir	• Reproduction primarily from seed (vs. vegetative) (though shortleaf and pitch pine can produce sprouts) • Small seeds require receptive seedbeds for germination and initial survival (e.g., mineral soil) • Slow growth relative to sprouts of hardwoods • Lower shade tolerance than competing hardwood species
Competitive advantages of limiting species	• Long-lived • High shade tolerance; can survive decades in the understory and respond to canopy disturbance	• Long-lived • Bark thickness insulates cambium during fire • Shortleaf pine and pitch pine sprout after fire

Temperate mixedwood forests

We selected five temperate mixedwood compositions across multiple regions for this assessment (Fig. 1). Two of these, eastern hemlock – hardwood and spruce–fir–hardwood, are characterized by shade-tolerant, late-successional softwood species. These are maintained by frequent, small-scale disturbances from mortality of single trees or small groups of trees, with periodic moderate-scale disturbances from insect outbreaks or weather events such as hurricanes (Frelich and Lorimer 1991; Seymour et al. 2002; D'Amato et al. 2018). Natural regeneration tends to range from fairly continuous to episodic, benefiting from multiple release events caused by low-severity canopy disturbances (Foster 1988; Fraver and White 2005; Kneeshaw and Prévost 2007). Though these compositions can be maintained by natural disturbances, some (e.g., spruce – fir – red maple on poorly drained sites) are the result of targeted softwood harvesting at intensities and frequencies greater than prevailing natural disturbance regimes (Seymour et al. 2002). This interferes with natural successional dynamics and hinders the long regeneration and recruitment processes of dominant shade-tolerant softwood species, leading to increased hardwood composition (Fortin et al. 2003; Barrette and Bélanger 2007; Boucher et al. 2009).

In contrast, shortleaf pine – oak, pitch pine – oak, and eastern white pine – oak mixedwoods are characterized by a softwood component of low to intermediate shade tolerance. These pine–oak mixtures require disturbances of at least moderate frequency or severity to recruit limiting pine species (Hibbs 1982; Stambaugh et al. 2007). Shortleaf pine – oak and pitch pine – oak are maintained by periods of frequent surface fires for pine establishment, followed by periods of infrequent but more severe fires, blowdowns, or other canopy disturbances during which pine recruitment occurs (Little 1979; Stambaugh et al. 2007). In these mixedwood forests, changes in fire regime (i.e., very frequent fire causing mortality of young pine seedlings) combined with timber harvesting (i.e., removal of pine seed source) have interfered with regeneration and recruitment of fire-adapted pine species (Record 1910; La Puma et al. 2013; Guldin 2019).

Dynamics of eastern white pine in mixture with oak are somewhat different. Eastern white pine can recruit naturally after moderate disturbances such as canopy gaps caused by wind, insects, diseases, or fire (Hibbs 1982; Abrams 2001). However, many stands today are legacies of land use, particularly agricultural clearing followed by abandonment and old-field colonization (Buttrick 1917; Foster 1995). Changes in fire regimes, combined with timber harvesting, difficulties with interfering vegetation, browsing by white-tailed deer (*Odocoileus virginianus*), and effects of white pine weevil (*Pissodes strobi*) and white pine blister rust (*Cronartium ribicola*), can make this forest composition difficult to maintain without careful management (Lancaster and Leak 1978; Ostry et al. 2010). All five of these mixedwood compositions are ecologically and economically important and offer a range of silvical properties and disturbance regimes for consideration.

Hemlock–hardwoods

Hemlock–hardwoods are found in the western Great Lakes through northeastern US and the St. Lawrence basin of Canada (Fig. 1). In the northern US, hemlock mixedwoods covered more than 4.1 million hectares in 2017 (USDA Forest Service 2019; Vickers et al. 2021). Eastern hemlock dominates the softwood component, but other softwoods such as eastern white pine, red and white spruce (*Picea rubens* Sarg. and *Picea glauca* (Moench) Voss, respectively), balsam fir, and northern white-cedar (*Thuja occidentalis* L.) can be found in varying amounts. The hardwood component is often dominated by sugar maple (*Acer saccharum* Marshall), American beech (*Fagus grandifolia* Ehrh.), or yellow birch (*Betula alleghaniensis* Britton). Other hardwoods occurring in lesser amounts include American basswood (*Tilia americana* L.), American elm (*Ulmus americana* L.), white ash (*Fraxinus americana* L.), northern red oak (*Quercus rubra* L.), black

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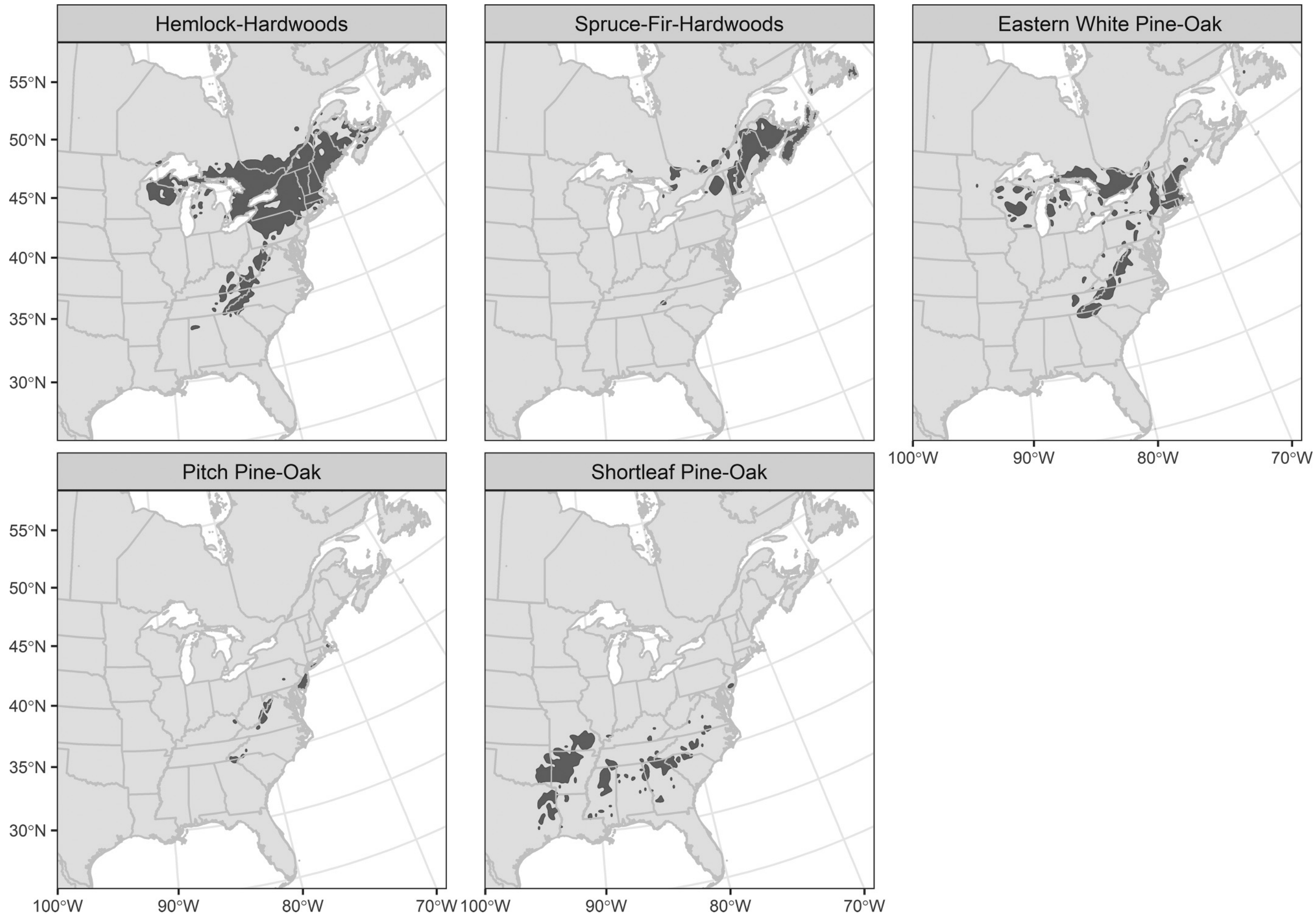
Fig. 1. Current distribution of temperate mixedwoods discussed in this paper in central and eastern North America. Maps were created using data from the USDA Forest Service (2019) and Canadian Forest Service (Beaudoin et al. 2017) with the sf (Pebesma 2018), raster (Hijmans 2020), and smoothr (Strimas-Mackey 2020) packages for R statistical software (R Core Team 2020). Administrative boundaries were obtained from GADM data (https://gadm.org/) via the raster package (Hijmans 2020) for R. Mixedwood labels are based on the dominant softwood (and hardwood, if applicable) in the mixture; the map for spruce–fir–hardwoods depicts mixedwoods where red spruce is the dominant softwood and balsam fir is present.



cherry (*Prunus serotina* Ehrh.), and red maple. Hemlock–hardwoods are frequently found at low to mid elevations; typical habitats are upland, well-drained, and moist, and soils are commonly loamy (Frothingham 1915; Nichols 1935; Dyer 2006).

Prior to European settlement, hemlock–hardwood forests had complex age and size structures resulting from varying intensities of canopy disturbances (Lorimer 2001; Lorimer and White 2003). Frequent, low-intensity wind events and localized insect and pathogen damage are often the prevailing natural disturbances and result in small canopy gaps that perpetuate shade-tolerant species. Infrequent, high-severity wind and ice storm events perpetuate species of lower shade tolerance. Today, hemlock–hardwoods in the US are often even aged, originating after extensive, heavy harvesting beginning in the late 1800s (Lorimer and Frelich 1994; Lorimer 2001; D'Amato et al. 2008). In managed forests today, partial harvesting of hemlock–hardwoods is common, and silvicultural treatments include thinning, selection cutting, and group/patch or irregular shelterwood cutting (Raymond et al. 2009; Kern et al. 2014; Leak et al. 2014).

Spruce–fir–hardwoods

Forests of red spruce in mixture with balsam fir and hardwoods are most abundant in the Appalachian region of the northeastern US, Quebec, Ontario, and the Canadian Maritimes across a range of landscape positions, from low and high elevations, with composition varying according to soils and management history (Fig. 1). Red spruce and (or) fir–hardwood mixtures covered over 4 million hectares of the northern US in 2017, with red spruce as the dominant softwood on almost 1.4 million of those hectares (USDA Forest Service 2019; Vickers et al. 2021). Dominant conifers are shade-tolerant spruce and fir in mixture with northern white-cedar (*Thuja occidentalis* L.) and (in the US) eastern hemlock. Companion hardwoods represent a broad spectrum of shade tolerance, from intolerant trembling and bigtooth aspen (*Populus tremuloides* Michx. and *Populus grandidentata* Michx., respectively) and paper birch (*Betula papyrifera* Marshall) to mid-tolerant yellow birch and tolerant red and sugar maple and American beech. In the southern Appalachians, spruce–hardwoods were historically more prevalent but have been greatly reduced by harvesting and are a focus of restoration efforts (Thomas-Van Gundy et al. 2012).

Spruce–fir–hardwoods occur throughout the northern Appalachian region but predominantly on mid-slope positions and in lowlands traditionally termed "spruce flats" (Westveld 1930). The mixtures occurring on mid-slope positions have well-drained, deep, moist soils and include sugar maple, yellow birch, and American beech. They can persist in the absence of management due to underlying site variability and small- to moderate-scale natural disturbances (Bouchard et al. 2006; Kneeshaw and

Prévost 2007). In contrast, mixedwoods on poorly drained, low-productivity spruce flats tend to be the result of repeated (1800s to present day) selective harvesting of spruce and other softwoods (Seymour 1992), a practice that converted former softwood stands to low-quality mixedwoods (Westveld 1930; Kenefic 2016). Hardwood species in these mixedwoods tend to be red maple (often stump sprouts), paper birch, and aspen. Even in the absence of management, mixedwood composition on lowlands can cycle between hardwood and softwood dominance due to fir mortality during periodic spruce budworm outbreaks (Amos-Binks and MacLean 2016).

Eastern white pine – oak

Eastern white pine – oak mixedwoods largely occur in south-central New England, with the greatest prevalence in Massachusetts, New Hampshire, and Maine, and in the Great Lakes region on both sides of the US–Canada border (Fig. 1). These mixtures covered close to 4.1 million hectares of the northern US in 2017 (USDA Forest Service 2019; Vickers et al. 2021). Eastern white pine – oak mixedwoods occupy the "transition hardwood zone" between oak–hickory (*Carya*) dominated central hardwood forests in the south and sugar maple – hemlock dominated northern hardwood forests to the north (Westveld et al. 1956). Mid-tolerant eastern white pine and shade-tolerant eastern hemlock are the main softwoods in these forests, with a wide range of hardwoods including mid-tolerant northern red and white oak (*Quercus alba* L.), yellow and black birch (*Betula lenta* L.), and white ash and shade-tolerant red maple.

Mixtures of eastern white pine and oak were a minor component of New England prior to European settlement (Abrams 2001), with contemporary abundance largely related to the ability of eastern white pine to dominate areas following agricultural abandonment in the 1800s and early 1900s (Cline and Lockard 1925). The majority of contemporary eastern white pine – oak mixedwoods developed following logging of these "old field" pine forests, with the hardwood components originating from advance reproduction that developed beneath the pine overstory (Kelty 1996). Given the influence of past land use on their current distribution, these mixedwoods occur across a range of sites; however, maintenance of their mixed nature is most readily achieved on dry-mesic to mesic glacial till soils (Cline and Lockard 1925; Goodlet 1960). Mixedwoods occurring on nutrient-poor sands and ridgetops tend toward eastern white pine dominance; oak stands on ridges in the Cumberland Plateau have been observed to transition to eastern white pine due to the buildup of advance reproduction of that species in the absence of fire (Blankenship and Arthur 1999). In contrast, hardwoods tend to predominate in eastern white pine – oak mixedwoods on mesic, fine-textured soils (Cline and Lockard 1925). On the latter sites, abundant hardwood competition presents a substantial challenge to maintaining eastern white pine in the canopy of mixedwood stands. Historical accounts suggest that this species naturally developed as scattered, dominant individuals as opposed to the higher current stocking attributed to past land use (Hibbs 1982; Fahey and Lorimer 2014).

Pitch pine – oak

Pitch pine – oak mixedwoods are best represented on sandy, nutrient-poor soils of the Atlantic coastal plain in the pine barrens of New Jersey, sand plains of Long Island, New York, and Cape Cod, Massachusetts (Fig. 1). Pitch pine – oak mixedwoods also occur on exposed xeric ridgetops throughout the Appalachians (Little and Garrett 1990; Williams 1998) and isolated xeric glacial outwash deposits (e.g., the Albany pine bush). Pitch pine is the dominant pine, with shortleaf, Virginia, loblolly (*Pinus taeda* L.), and Table Mountain (*Pinus pungens* Lamb.) pine also occurring; all are shade intolerant. In sum, pitch pine – oak mixedwoods covered approximately 0.3 million hectares of the northern US in 2017 (USDA Forest Service 2019; Vickers et al. 2021). Dominant oak species are primarily white and red oaks of intermediate shade tolerance, including chestnut (*Quercus prinus* L.), white, black (*Quercus velutina* Lam.), scarlet (*Quercus coccinea* Münchh.), southern red (*Quercus falcata* Michx.), and northern red oak. More xeric, fire-prone sites include pitch and shortleaf pine with post (*Quercus stellata* Wangenh.), blackjack (*Quercus marilandica* Münchh.), scrub (*Quercus ilicifolia* Wangenh), and dwarf chestnut (*Quercus prinoides* Willd.) oak. Pitch pine with shade-tolerant red maple and blackgum (*Nyssa sylvatica* Marshall) occur on mesic sites of the Atlantic coastal plain (McCormick and Jones 1973).

Pitch pine – oak mixedwoods are an early successional forest type, and historical land use and disturbance have been major factors in their formation and persistence. Before European settlement, pitch pine – oak mixedwoods were likely maintained by low- to moderate-intensity fires resulting from lightning or Native American practices (Lorimer and White 2003). Contemporary pitch pine – oak mixedwood stands regenerated following intensive harvesting, charcoaling activities, and agricultural use and then abandonment following European settlement. High-intensity wildfires in the late 1800s and early 1900s resulted in a period of expansion of pitch and shortleaf pine (Little 1979; Forman and Boerner 1981; Stambaugh et al. 2018). Wildfire suppression starting in the 1930s increased oak regeneration and accelerated succession toward hardwoods in pitch pine – oak mixedwoods (La Puma et al. 2013). More recently, increased use of prescribed burning has facilitated pine regeneration, which is dependent on litter layer disturbance for successful establishment (Little and Garrett 1990).

Shortleaf pine – oak

Shortleaf pine is found in mixture with hardwoods (predominantly oak) across 22 states in the central, southern, and eastern US but is particularly abundant in western portions of the central states (Fig. 1) (Moser et al. 2007; Oswalt 2012). In this region, shortleaf pine – oak mixedwoods include a variety of oak species such as white, black, post, northern red, scarlet, and southern red oak and are found on upland sites with well-drained soils, often of relatively low productivity (Mattoon 1915). Shortleaf pine mixedwoods covered almost 0.4 million hectares of the northern US in 2017 (USDA Forest Service 2019; Vickers et al. 2021). The presence of shortleaf pine – oak mixtures is associated with excessively drained and acidic stony soils formed from sandstone or cherty limestone, often on dry south- and west-facing slopes or ridges (Fletcher and McDermott 1957).

Changes in disturbance regimes have reduced the abundance of shortleaf pine across the landscape and shifted mixedwoods toward hardwood dominance (Guyette et al. 2007; Ojha et al. 2019). Historically, fire has been an important disturbance for maintaining shortleaf pine – oak mixtures. Shortleaf pine can regenerate following stand-replacing fires (Keeley and Zedler 1998) or low-severity surface fires of moderate frequency (e.g., 8- to 15-year intervals) (Stambaugh et al. 2007). Widespread fire exclusion policies from around the 1930s, following a period of exploitive timber harvesting and frequent burning in the late 1800s and early 1900s, resulted in loss of both mature, seed-bearing shortleaf pine in the canopy and new pine germinants (Batek et al. 1999; Guyette et al. 2007). Over time, difficulties with shortleaf pine regeneration have resulted in a gradual transition of both shortleaf pine and mixedwood stands to hardwoods (Olson et al. 2017).

Common features and challenges

Though the temperate mixedwood forests described here occur across a broad geographic range and comprise different species, there are commonalities in mixedwood ecology, regeneration, and stand development (Table 1). Notably, one or more softwood species in each of the five types (i.e., eastern hemlock, red spruce, northern white-cedar, eastern white pine, pitch pine, and shortleaf pine) are difficult to regenerate and recruit in mixture, thus acting as limiting

Table 2. Regeneration problems, limiting and complicating factors, and silvicultural solutions for selected temperate mixedwoods.

	Mixedwoods with softwoods of high shade tolerance	Mixedwoods with softwoods of low to intermediate shade tolerance
Regeneration problem	• Anthropogenic disturbances (e.g., timber harvesting) deplete seed sources and interfere with natural succession, thereby hindering the long regeneration and recruitment processes of limiting softwoods	• Changes in fire regimes combined with timber harvests interfere with regeneration and recruitment processes of limiting softwoods • Some stands are artefacts of agricultural abandonment, a condition difficult to replicate today (e.g., eastern white pine – oak in New England)
Limiting factors	• Harvesting has increased hardwood litter and decreased deadwood, reducing germination of limiting softwoods • Interspecific competition, particularly from hardwoods	• Deep litter layer without fire reduces germination, particularly for pitch and shortleaf pine • Interspecific competition, particularly from hardwoods
Complicating factors	• Rich site conditions favor hardwood competition • Browsing reduces recruitment of limiting softwoods to sapling size • Episodic outbreaks of damaging insects (e.g., spruce budworm) can cause growth reductions and mortality	• Rich site conditions favor hardwood competition • Browsing reduces recruitment of some limiting softwoods to sapling size (i.e., eastern white pine) • Damaging insects (e.g., white pine weevil and blister rust) can negatively impact vigor, form, and value
Silvicultural solutions	• Use regeneration methods that maintain seed sources and partial canopy cover (i.e., establish advance reproduction) • Disturb forest floor with mechanical methods to create receptive seedbeds for germination if advance reproduction is lacking • Plant seedlings in canopy openings if seed sources are lacking and natural regeneration is insufficient • Release limiting softwoods during recruitment with herbicide or mechanical cleaning • Manage species composition at each intervention • Manage limiting softwoods as "two-rotation" species	• Use regeneration methods that maintain seed sources and create large canopy openings to increase light levels in the understory • Disturb forest floor with prescribed fire or mechanical methods to create receptive seedbeds for germination • Plant seedlings if seed sources are lacking and natural regeneration is insufficient • Release limiting softwoods during recruitment with herbicide, mechanical cleaning, or properly timed prescribed fire • Modify species composition with intermediate treatments • Manage limiting softwoods as "two-rotation" species

Note: Limiting factors are those which prevent establishment or reduce likelihood of successful recruitment of limiting softwoods; complicating factors are those which affect the severity of limiting factors.

species. Regardless of mixedwood composition, limiting factors for desired softwoods include small seeds, narrow regeneration requirements, and interspecific competition, as well as depleted seed sources from past selective logging (Table 2). In the temperate–boreal ecotone, for example, eastern hemlock, red spruce, and northern white-cedar seedlings are disproportionately associated with moisture-holding deadwood or exposed mineral soil substrates (Weaver et al. 2009; Larouche et al. 2011). Yet, repeated harvests have preempted mortality (eliminating natural downed woody material) and increased proportions of hardwoods (and thus hardwood leaf litter), reducing availability of regeneration substrates favorable for these species (Weaver 2007). Similarly, a long history of fire exclusion in pine–oak mixedwoods has facilitated accumulation of deep litter layers that impede germination of the small-seeded pines (Grano 1949; Stambaugh et al. 2007). Fire exclusion in shortleaf pine or pitch pine mixedwoods has also supported the accumulation and development of dense hardwood advance reproduction. This dense hardwood reproduction prevents the accumulation of shortleaf pine reproduction (Guldin 2007) and responds vigorously to canopy openings created by harvesting or severe wind disturbances, leading to reduction or eventual elimination of the pine component (Guyette et al. 2007).

Additional complicating factors may further reduce regeneration success for limiting species (Table 2). Seedlings of limiting softwoods typically grow more slowly than hardwood sprouts, with competitive disadvantage exacerbated by site richness (Goodlet 1960; Seymour 1992). In several regions, selective herbivory of softwoods further constrains regeneration success (Vickers et al. 2019). Despite these challenges, the limiting softwoods have some advantages over competing vegetation. All are long-lived, with typical lifespans ranging from more than 200 years for shortleaf and pitch pine to more than 400 years for eastern white pine and red spruce, and even longer for eastern hemlock and northern white-cedar (Blum 1990; Godman and Lancaster 1990; Johnston 1990; Lawson 1990; Little and Garrett 1990; Wendel and Smith 1990). The latter three are highly shade tolerant and can persist in shaded understories for decades or longer before release (Cary 1894; Hough and Forbes 1943; Nelson 1951). This combination of longevity and ability to withstand suppression enables these shade-tolerant species to outlast competitors and ascend to the canopy over time (Dahir and Lorimer 1996; Fraver and White 2005; Ruel et al. 2014). As a species of intermediate shade tolerance, eastern white pine does not tolerate suppression for long periods of time and requires canopy opening for overstory recruitment, especially in mixture with more shade-tolerant species (Fajvan and Seymour 1993; Abrams 2001). Once this species has reached the canopy, it can persist for decades or longer (Abrams and Orwig 1996). All pine species of the three pine–oak mixedwoods have thick bark as mature trees, which insulates the cambium and reduces damage from fire. Shortleaf pine and pitch pine develop relatively thick bark as saplings, which provides protection against top-kill by fire and allows greater opportunity for canopy recruitment if competing hardwoods are top-killed (Fan et al. 2012; Gallagher 2017). Moreover, both species are capable of basal and epicormic sprouting following fire (Lawson 1990; Little and Garrett 1990). Generally, shortleaf pine sprouts more readily from the base during the seedling and sapling stages, while pitch pine can sprout readily from the base or stem. In both cases, sprouting provides a mechanism for persistence under a regime of fire (Bond and Midgley 2001; Pausas 2015).

Silvicultural systems for mixedwood stands

Silvicultural systems include planned treatments throughout all stages of stand development. In mixedwood systems, this requires attention to processes of tree regeneration, growth, and mortality for mixtures of species with different shade tolerances, growth rates, longevities, and regeneration mechanisms (Kabrick et al. 2017). As a refinement of this general recommendation, we propose that stand structure and composition must be managed at each entry to maintain vigorous trees of limiting species through time. Regardless of whether regeneration occurs periodically (i.e., in multi-aged systems) or at the end of a rotation (i.e., in even-aged systems), silvicultural systems for temperate mixedwoods should maintain limiting species as growing stock and seed sources (e.g., Boulfroy et al. 2012; Carter et al. 2017), provide an appropriate seedbed for germination (e.g., Larouche et al. 2015), and moderate light and growing conditions to favor their development from seedling establishment through canopy ascension (e.g., Raymond and Bédard 2017; Raymond et al. 2018). Abundance of the hardwood component and its relatively high regeneration potential and competitive ability usually provide ample opportunity for its persistence and dominance (e.g., Guyette and Dey 1997; Fei and Steiner 2007).

Multi-aged silvicultural systems such as selection and irregular shelterwood usually aim at multiple goals at each intervention (e.g., regeneration and tending), while maintaining continuous seed sources. These systems are useful in management for multiple species if stand structures and compositions permit their application (Raymond et al. 2009). Appropriate silvicultural systems vary among the mixedwood compositions described here but have some common characteristics. Where removal of most or all of the overstory is desired, some level of canopy cover of limiting softwoods is generally necessary to provide seed or modify microenvironments for regeneration establishment (Fig. 2). During periods of regeneration, silvicultural systems for mixedwoods with a shade-tolerant softwood component can retain relatively high residual stand density for a long period, e.g., irregular shelterwood or group selection. Those for mixedwoods with softwoods of intermediate to low shade tolerance usually retain a relatively low residual stand density for a short period, e.g., seed tree or regular shelterwood, though variants of irregular shelterwood and group selection can also be effective (Fig. 2). In the case of eastern white pine – oak, irregular shelterwood and group selection systems with residual densities and gap sizes falling between those for shade-tolerant or -intolerant species are more favorable than systems with a higher or lower level of canopy closure, given the light requirements of this species as well as the increased risk of damage from white pine weevil in open conditions (Ostry et al. 2010).

In all cases, seed trees of limiting species should be retained through the regeneration period or longer (e.g., Carter et al. 2017). Where slow-growing and long-lived species such as eastern hemlock, red spruce, northern white-cedar, or eastern white pine are in mixture with short-lived hardwoods (e.g., paper birch or aspen) or softwoods (e.g., balsam fir), retaining some trees of limiting softwoods for more than a single rotation of shorter lived species will provide insurance against regeneration failure and allow additional volume and value accrual (Boulfroy et al. 2012). As such, shade-tolerant limiting softwoods can be characterized as two-rotation species (Seymour 1992).

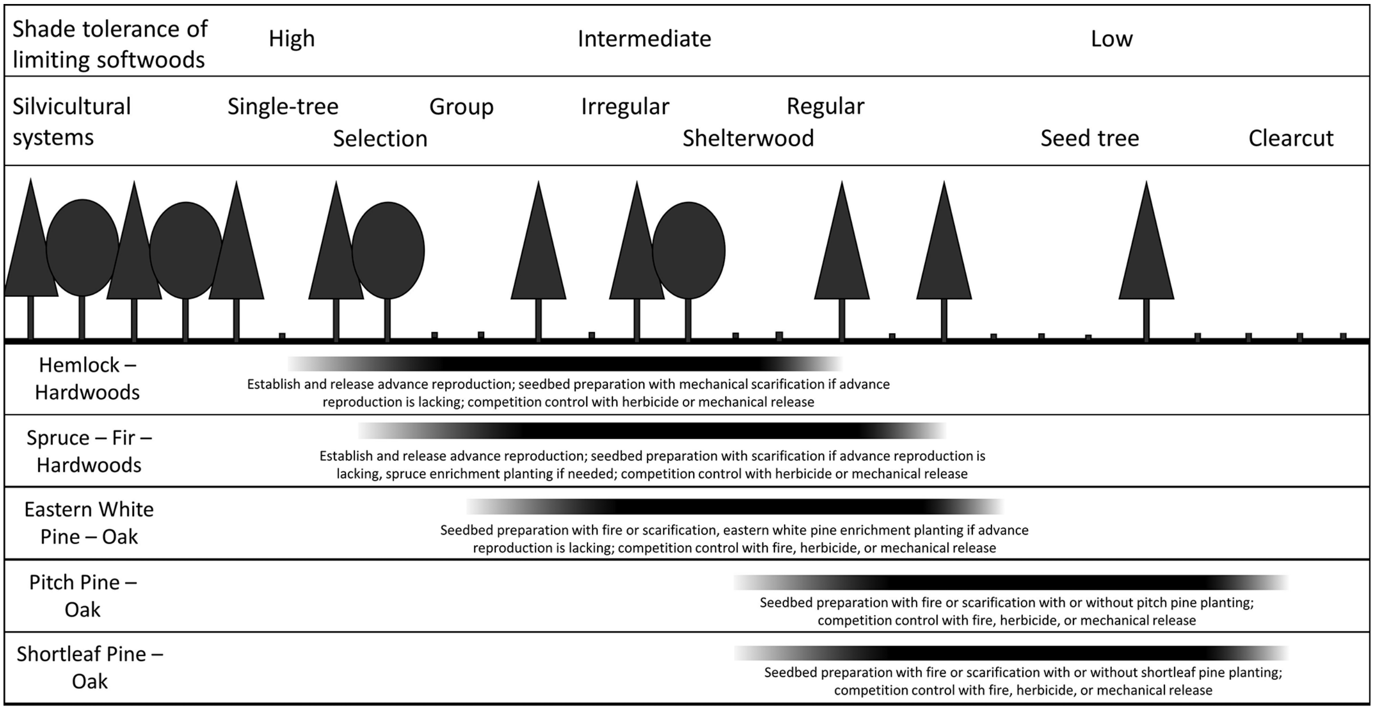
Diversifying light levels across a stand can facilitate development of mixtures in which shade tolerances of desired species vary (Raymond and Bédard 2017; Raymond et al. 2018). In mixedwoods comprising shade-tolerant softwoods, appropriate systems provide protection for seedlings of limiting softwoods during establishment, while subsequent interventions increase light beneath the canopy by further reducing overstory stocking or increasing gap size after establishment. As long as such treatments do not disproportionately favor competitors, survival and growth of shade-tolerant reproduction will likely improve, because optimal conditions for sapling growth often differ from those for seedling establishment (Raymond et al. 2006; Larouche et al. 2011; Dumais et al. 2020). In eastern hemlock – hardwood stands of the Great Lakes region, for example, Webster and Lorimer (2005) observed that canopy gaps of 200 to 1000 m^2 were effective for maintaining species with a range of shade tolerances, with mid-tolerant species such as yellow birch favored in gaps > 250 m^2. In spruce–hardwoods, Raymond et al. (2018) found that 100–250 m^2 gaps had higher densities of yellow birch than red spruce reproduction, though Dumais and Prévost (2014) observed favorable growth of red spruce in openings of that size. Regardless of opening size, carefully selected trees can be retained within gaps for seed, growing stock, or biodiversity conservation (Carter et al. 2017; Kern et al. 2017; Knapp et al. 2019). The appropriate level of within-gap live-tree retention will vary depending on gap size and shade tolerance of desired reproduction (D'Amato et al. 2015).

Clearcutting or seed tree methods have been recommended for regeneration of shade-intolerant softwoods such as shortleaf and pitch pine (Yocom and Lawson 1977; Garrett and Fleming 1983; Lawson and Kitchens 1983), though shelterwood systems may be favored to increase seed production and improve initial establishment (Little and Moore 1950; Guldin 2019). The partial shade created by higher density shelterwoods does not appear to reduce survival or early growth of these species if canopy closure is later reduced. In shortleaf pine – oak stands, for example, Kabrick et al. (2015) found that residual overstory density in shelterwoods did not significantly reduce survival of shortleaf pine seedlings during the first 5 years after planting in harvested oak stands. Although increasing residual overstory significantly decreased growth of all reproduction, shortleaf pine seedlings maintained growth rates similar to those of hardwood competitors. In contrast, extended and irregular shelterwood systems are suitable for regenerating mixedwoods composed of mid-tolerant softwoods such as eastern white pine, given the ability of these systems to discriminate against faster growing shade-intolerant hardwoods and allow for development of large softwood advance reproduction prior to overstory removal. In eastern white pine – oak mixedwoods in New England, for example, eastern white pine saplings predating establishment cuttings were better able to outcompete hardwoods than eastern white pine established during shelterwood treatments (Kelty and Entcheva 1993). As such, efforts to maintain eastern white pine as part of these mixedwoods have often focused on protecting and releasing advance reproduction (Kelty 1996) or underplanting prior to shelterwood treatments to develop this component for subsequent release (Smidt and Puettmann 1998). Advance reproduction is also the most reliable means of securing the presence and competitive advantage of shade-tolerant softwoods such as red spruce (Westveld 1930; Moores et al. 2007), eastern hemlock (Hough and Forbes 1943), and northern white-cedar (Boulfroy et al. 2012).

Seedbed for germination

Limiting species within the mixedwoods discussed here commonly require specific seedbed conditions for germination, and regeneration failures can occur if seedbed conditions are not suitable. For example, contact with mineral soil greatly improves germination of shortleaf, pitch, and eastern white pine (Boggs and Wittwer 1993; Raymond et al. 2003; Yocom and Lawson 1977). While eastern hemlock (Eckstein 1996), red spruce (Moore 1926), and northern white-cedar (Larouche et al. 2011) also germinate well in exposed mineral soil, germination of shade-intolerant hardwood competitors also increases (e.g., Larouche et al. 2015). If exposed or mixed mineral soil is desired, soil disturbance can result from harvesting operations but more commonly requires site preparation via mechanical scarification (Prévost et al. 2010; Willis et al. 2015; Kern et al. 2017; Kern et al. 2019) or prescribed burning (Yocom and Lawson 1977; Clabo and Clatterbuck 2015).

Fig. 2. Conceptualization of silvicultural systems for maintaining limiting species in five mixedwood compositions, with additional treatment considerations for regeneration and recruitment.



Where decayed deadwood is present, small-seeded red spruce, eastern hemlock, and northern white-cedar (as well as companion hardwood yellow birch) germinate well on this moisture-holding organic substrate (Simard et al. 2003; Weaver et al. 2009; Raymond and Bédard 2017). In mixedwood stands where these species are limiting, deadwood retention and recruitment can be facilitated (Cornett et al. 2001; Marx and Walters 2008). Existing deadwood can be conserved through preharvest designation of machinery trails and winter harvests to avoid or minimize damage to this substrate during timber extraction. In the long-term, permanently retaining some large trees, which will eventually die and fall over, is a logical step to help replenish deadwood pools (Weaver et al. 2009).

Enrichment planting

Where successful natural regeneration is unlikely, planting may be important for establishing limiting species in mixedwoods. Enrichment planting, used to restore or increase density of desired species where advance reproduction is insufficient, can help to reach long-term composition objectives (Paquette et al. 2006). This approach has proven effective for establishing shortleaf pine (Kabrick et al. 2015; Clabo and Clatterbuck 2020), eastern white pine (Raymond et al. 2006), and red spruce (Hébert et al. 2013; Dumais et al. 2019; Dumais et al. 2020). Planting can be integrated with the appropriate silvicultural system for the forest type (Fig. 2) to bypass reliance on seed supply and seedbed conditions needed for natural regeneration. In spruce–fir–hardwood stands, for example, enrichment planting in gaps seems promising in irregular shelterwood and hybrid selection systems (Dumais et al. 2019), though release from competition is important when understory vegetation is abundant (Dumais et al. 2020). In the Missouri Ozarks, the height of planted shortleaf pine seedlings fell behind that of competing hardwoods (which likely regenerated by sprouting) due to slow early growth after planting (Kabrick et al. 2015). In pitch pine – oak mixedwoods where high-intensity prescribed burns are not possible, mechanical thinning followed by the addition of biochar has increased seedling growth and water use efficiency (Licht and Smith 2020).

Controlling competition and stand development

Treatments applied during stand development can modify stand composition by releasing desired species from competition. Without such interventions, high levels of interspecific competition common in mixedwood forests can negatively impact growth and survival of limiting species. In mixedwood spruce–fir–hardwood stands, red spruce is often outcompeted by balsam fir and hardwoods (Westveld 1928, 1930). Failure to control competition through release of red spruce early in stand development can result in both slower growth and a lower proportion of this species. Spruce abundance 30 years after initiation of the shelterwood system in spruce–fir–hardwood stands in Maine, for example, was two to three times lower in unthinned than precommercially thinned stands where spruce release had been prioritized (Granstrom 2019).

In shortleaf pine – oak mixedwoods, planted shortleaf pine seedlings and saplings often grow more slowly than hardwood competitors originating from sprouts (Kabrick et al. 2015). If not released within 5 to 8 years of stand establishment, suppressed shortleaf pine saplings have a high probability of mortality (Lyczak 2019). Repeated low-intensity surface fires, typically at 5- to 8-year intervals in shortleaf pine – oak or pitch pine – oak mixedwoods, increase the probability of pine seedling recruitment and sapling survival by reducing competition from hardwoods and shrubs (Little 1979; La Puma et al. 2013; Stambaugh et al. 2007, 2019). The timing of prescribed fire has been shown to increase the competitiveness of shortleaf pine relative to associated hardwoods within the regeneration layer (Fan et al. 2012) due to interspecific differences in resistance to top-kill. Clabo and Clatterbuck (2019) recommend waiting until shortleaf pine is at least 3 years old before burning to reduce likelihood of top-kill or mortality; they also found that release with a combination of herbicide and prescribed fire favored development of shortleaf pine – oak mixtures following artificial regeneration (Clabo and Clatterbuck 2020). Mean fire return interval is essential in maintaining pitch pine – oak mixedwoods in the New Jersey Pinelands. Following seedling establishment, a fire-free period reduces mortality, while subsequent surface fires at relatively frequent intervals reduce competition from understory oaks and shrubs (Little et al. 1948; Little and Somes 1961; La Puma et al. 2013).

Specific release treatments vary among forest compositions and in accordance with local stand conditions. Broadcast herbicide treatments that target broadleaf species have been used to promote softwood dominance in naturally regenerated and planted forests (Olson et al. 2012; Burgess et al. 2010); however, such treatments may not be necessary, feasible (i.e., due to similar susceptibilities among desired and undesired species), or permitted. Cut-stump, stem injection, or targeted foliar or basal spray application of herbicides could be used to selectively remove competing hardwoods in mixedwoods (Kenefic et al. 2014), but non-target deposition can occur (Nowak and Ballard 2005). Among the mixedwood compositions that we examined, hardwood species commonly sprout following disturbance, suggesting that properly timed mechanical release (brushing) may provide regenerating softwoods competitive advantage while not eliminating the hardwood component of the stand (Prévost and Charette 2017).

Thinning treatments (often precommercial thinning) can also be used to manage the compositional balance of hardwood and softwood species based on management objectives. Such treatments may be applied across even-aged stands or within gaps in multi-aged stands. In spruce–fir–hardwoods, for example, precommercial release by mechanical (brushsaw) or chemical (basal spray) means has proven effective for increasing proportions and growth of red spruce while maintaining mixedwood composition of multi-aged stands (Prévost and Charette 2017; Kenefic et al. 2014; Puhlick et al. 2019). In eastern white pine – oak mixedwoods, outcomes of release treatments vary across sites types, with application most effective on well-drained, nutrient-poor sites where a single release treatment at the sapling stage may effectively maintain and enhance the eastern white pine component (Goodlet 1960). In contrast, repeated weeding and cleaning treatments are required on higher quality sites to sustain an eastern white pine component relative to fast-growing hardwood species (Fisher and Terry 1920).

Commercial thinning in even-aged stands or tending immature age classes in multi-aged stands also provides opportunities to release limiting species from competition and improve their vigor and growth. Though the primary objective of intermediate treatments such as these is to increase resources available to residual trees, reductions in stand density can initiate regeneration of shade-tolerant species. In stands dominated by red spruce and balsam fir, for example, Olson et al. (2014) found that commercial thinning not only increased tree-level growth and yield but also increased density of advance reproduction. They further observed higher seedling densities, rates of recruitment, and proportions of hardwoods in stands where thinning intensity was greater. Commercial thinning can also be used to capture mortality of short-lived species in stands where desired species are not yet mature, e.g., balsam fir or paper birch in spruce–fir–hardwood stands (Seymour 1992). In shortleaf pine – oak mixedwoods of the Missouri Ozarks, black and scarlet oaks are commonly removed at approximately 70 years old due to declining health; this favors development of mixtures of longer lived white oak and shortleaf pine (Olson et al. 2017). These strategies exemplify the linkages between treatments in silvicultural systems and the need to consider multiple aspects of mixedwood stand development at each intervention.

Complicating factors

The degree to which regeneration and recruitment of limiting species may challenge mixedwood management is often moderated by external, complicating factors such as site quality and browsing by deer or snowshoe hare (*Lepus americanus*) (Table 2). As site productivity increases, hardwood species generally become more abundant or more competitive, and limiting softwood species become more difficult to regenerate (Brinkman and Rogers 1967; Smidt and Puettmann 1998; Westveld 1953). As a result, silvicultural prescriptions should be tailored to site conditions. On more productive sites, release treatments (e.g., after overstory removal in even-aged stands or in portions of multi-aged stands where competition is high) may need to be of greater intensity, applied earlier, or repeated more often to allow limiting softwood species to reach competitive stature.

For some species and forest types, abundant ungulate populations create problems due to intensive browsing (McWilliams et al. 2018). Northern white-cedar, for example, is a critical winter browse species for deer, and overbrowsing has been implicated in range-wide regeneration and recruitment failures (e.g., Heitzman et al. 1999; Larouche et al. 2010). In the Northeast and Great Lakes regions, eastern white pine seedlings are susceptible to browsing, with growth reductions and mortality observed in both pure and mixed stands where deer populations are high (Saunders and Puettmann 1999; Ward and Mervosh 2008; White 2012). In the western Great Lakes and some parts of the Northeast, deer browsing on eastern hemlock has also severely limited recruitment (Rooney et al. 2000; Long et al. 1998). In addition to reducing populations of herbivores through hunting or excluding their access by fencing, silvicultural treatments and forest operations can be adapted to create physical barriers using tree tops and branches left after harvesting (Grisez 1960; Verme and Johnston 1986; Smallidge and Chedzoy 2019), grow seedlings of desired species in mixture with other palatable species to distribute effects of browsing (Herfindal et al. 2015), or release saplings of vulnerable species to accelerate growth above browsing height (Boulfroy et al. 2012). These methods have yielded inconsistent results, and mixedwood management in areas where limiting softwoods are preferred browse species might be most successful at times and in places where local populations of herbivores are low (Boulfroy et al. 2012).

Damaging insects further complicate efforts to manage mixedwood composition and can be advantageous or disadvantageous to limiting softwood species. Episodic outbreaks or endemic populations of native and nonnative insects can — depending on species and outbreak severity — result in damage ranging from temporary growth reductions to mortality. Hemlock woolly adelgid (*Adelges tsugae*), for example, has caused widespread mortality of eastern hemlock in the southern Appalachians, shifting many hemlock–hardwood stands to a predominantly hardwood composition dominated by maple, birch, beech, or oak (Ford et al. 2012). While there are few silvicultural options other than pre-salvage for reducing mortality in hemlock woolly adelgid infested stands (Orwig and Kittredge 2005), silvicultural treatments can be used to reduce impacts of some damaging insects. For example, extended irregular shelterwood is recommended to minimize damage from white pine weevil in eastern white pine (Livingston et al. 2019) and can be effective for mixedwood management. In contrast, damaging insects affecting competing species may have favorable impacts on limiting softwoods (e.g., Seymour 1992; Ruel et al. 2014). The degree to which limiting softwoods and their competitors are affected by damaging agents — and how mixedwood composition might alter these relationships (MacLean and Clark 2021) — should be considered in development of appropriate silvicultural systems.

Conclusion

Temperate forests with mixedwood compositions are common across central and eastern North America and provide a variety of ecosystem services and commodity-production benefits. Despite their abundance, silviculture in mixedwood stands is often challenged by problems with regeneration or recruitment of desired softwoods and different growth rates and longevities of component species. We synthesized information regarding the current state of knowledge for five temperate mixedwood compositions in two broad categories: those with shade-tolerant softwoods perpetuated by frequent small to infrequent moderate canopy disturbances, and those with mid shade tolerant to shade intolerant softwoods maintained by more frequent, moderate to severe canopy disturbances and (or) surface fires.

All of these mixedwoods tend to transition to pure hardwood or softwood compositions if the disturbance regimes that promoted the species mixtures are modified. As a consequence, management of these mixedwood compositions must include attention to limiting species, usually softwoods with specific seedbed and regeneration requirements. Competition from more prolific and faster growing hardwoods is common, as are complicating factors such as site quality, level of herbivory, and damaging insects. Nevertheless, management approaches that sustain mixedwood composition can be developed. Silvicultural systems that maintain seed sources of limiting species and suitable microenvironmental conditions for regeneration are recommended for each mixedwood type; most provide at least partial canopy cover during regeneration. Protection of advance reproduction and competition control through early stand tending are recommended, with modifications of treatments as needed due to complicating factors. Importantly, sustainability of mixedwood composition is not determined solely by treatments applied during discrete periods of regeneration and recruitment; structure and composition must be managed at each entry to maintain species with different growth rates and longevities and accumulate advance reproduction or seed-producing trees. Though the mixedwoods for which silvicultural recommendations are presented in this paper represent only a small portion of temperate hardwood–softwood forests in North America, considering disturbance dynamics and silvical properties (e.g., shade tolerance, mode of regeneration, growth rate, and longevity) of important species is a useful approach to classifying mixedwood forests more generally. In doing so, we discovered commonalities among seemingly disparate forests related to species silvics, land use legacies, and complicating factors that can serve as a model for mitigating limiting factors to mixedwood management on a broader scale.

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