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Eastern Temperate Forests

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10 EASTERN TEMPERATE FORESTS

F.S. Gilliam, C.L. Goodale, L.H. Pardo, L.H. Geiser, E.A. Lilleskov

10.1 Ecoregion Description

The Eastern Temperate Forests ecoregion extends from the Atlantic Coast westward into eastern Texas, Oklahoma, Missouri, Iowa, and Minnesota. The ecoregion description is adapted from CEC (1997). Eastern Temperate Forests are comprised of two fairly distinct ecosystems: eastern hardwood forests and the Southeastern Coastal Plain. The former includes mixed wood plains and central plains, as well as Ozark and Ouachita-Appalachian forests of the northeastern and midwestern states and Appalachian Mountains. The latter is composed of the southeastern and coastal plains extending from Cape Cod and Long Island to Florida, inland to and around the Appalachian mountains (Fig. 2.2; CEC 1997).

The Eastern Temperate Forests ecoregion is distinguished by its temperate, humid climate; dense, diverse forest cover; and dense human population (>160 million). Coastal plains underlain by sedimentary bedrock in the southeast abut older sedimentary, metamorphic, and igneous bedrock of the Appalachian Mountains (peaking at > 2,000 m). Mixed limestone-dolomite plains and hills dominate the west central parts, sedimentary rock dominates the northwest plains and plateaus, and glacial activity shaped northern landscapes. Soils are mostly leached, being nutrient-poor to calcium-rich. Surface waters include abundant perennial streams, areas of high lake density, diverse wetlands, and rich maritime ecosystems. The climate grades latitudinally from cool, continental to subtropical. Summers are hot and humid (27 °C to 32 °C daily maxima); winters are mild to cool (-12 °C to 4 °C). Precipitation (100 to 150 cm yr⁻¹) is relatively even throughout the year, with summer or spring peaks.

10.2 Eastern Hardwood Forest

10.2.1 Ecosystem Description

Eastern hardwood forests, as originally described by Braun (1950) and further characterized by Greller (1988), are among the most diverse forests of North

America, particularly those of the mixed mesophytic forest region (Hinkle et al. 1993). Forest types range from beech-maple and maple-basswood in the east to mixed oak-hickory in the upper Midwest, and oak-hickory-pine in the Appalachians southward. Ashes (*Fraxinus* spp.), elms (*Ulmus* spp.), black cherry (*Prunus serotina*), yellow-poplar (*Liriodendron tulipifera*), sweet gum (*Liquidambar styraciflua*), basswood (*Tilia* spp.), hackberry (*Celtis occidentalis*), persimmon (*Diospyros virginiana*), eastern red cedar (*Juniperus virginiana*), and dogwood (*Cornus* spp.) are also wide ranging. The complex and diverse forest regions include: (1) the mixed mesophytic forest region; (2) the western mesophytic forest region; (3) the oak-hickory forest region; (3) the former oak-chestnut forest region; and (4) the oak-pine forest region (Braun 1950). Each of these regions displays an impressive number of canopy co-dominant species, and occupies widely ranging topography on numerous soil types derived from sharply contrasting parent materials. The herbaceous layer, most often defined as the stratum of vascular plants ≤1 m in height (Gilliam and Roberts 2003), can represent >90 percent of vascular plant species richness of temperate deciduous forest ecosystems in this ecoregion (Gilliam 2007).

10.2.2 Ecosystem Responses to N Deposition

Responses of eastern hardwood forests to excess nitrogen (N) deposition include increases in tissue N, soil N cycling, nitrate (NO₃⁻) leaching, decreases in soil carbon:nitrogen (C:N) ratio, and shifts in community composition, including declines in species richness and abundance. The stages of N saturation are described in Chapter 7. Some ecosystem responses occur as a result of acidification and therefore are caused by sulfate (SO₄⁻) as well as NO₃⁻. These responses include soil nutrient cation imbalances (particularly calcium (Ca) and magnesium (Mg)) from enhanced leaching of NO₃⁻, especially in soils derived from intermediate to acidic classes of parent material (Bailey et al. 2005). As the result of decreases in soil nutrient cation

availability, decreases in net primary productivity of forest ecosystems (i.e., forest decline) can occur. At the interface between terrestrial and aquatic habitats, excess N can cause increases in NO_3^- in streams and lakes and, particularly in extreme cases, increases in the mobilization of aluminum (Al^{3+}) in freshwater ecosystems (Driscoll et al. 2003).

Excess N deposition can also cause a loss of biodiversity. Gilliam (2006) identified five mechanisms to explain such loss: (1) alteration of interspecific competition; (2) increases in herbivory; (3) decreases in mycorrhizal infection; (4) increases in pathogenic fungal infection; and (5) enhanced likelihood of invasions by nonnative species. Herbaceous, epiphytic lichen, and bryophyte layers are generally most sensitive to a variety of disturbances, including chronically elevated N deposition.

Herbaceous species. Gilliam (2006) reported that the response of the forest herbaceous layer to increasing N may include the following: (1) initial increases in cover of the herb layer; (2) decreases in species richness resulting from loss of numerous N-efficient species; (3) decreases in species evenness resulting from increasing dominance of a few high N-requiring species; and (4) declines in forest biodiversity as a result of decreases in both richness and evenness. In addition, these studies suggest that the response time of herb layer species to increases in N availability is more rapid when ambient N deposition is low. Thus, a rapid response should occur in areas receiving low levels of atmospheric deposition of N, such as that found for Hurd et al. (1998) in the Adirondacks, whereas a delayed response would be expected in areas receiving high N deposition, such as that found by Gilliam et al. (2006a). This response pattern has been reported for other sites in eastern hardwood forests (Fraterrigo et al. 2009, Royo et al. 2010). The relationship between plant response time to added N and ambient N deposition could arise because the effect is ultimately a function of relative amounts of N added. For a given amount of N added, the relative addition would be higher for a site receiving lower amounts of ambient N deposition.

Still other work has focused on the importance of the herb layer in mediating N cycling (Gilliam 2007). Recent work (Moore et al. 2007, Muller 2003, Welch et al. 2007) has demonstrated that plants of the herb layer facilitate N cycling in a disproportionately large way compared to their minimal biomass. This is primarily because herb layer foliage is generally higher in nutrient content and more decomposable than tree foliage.

Lichens. Lichen community-level responses to changing sulfur dioxide (SO_2), acidity, and nutrient N deposition regimes vary. Increased deposition in low deposition areas results in species composition shifts to tolerant species, while in high deposition areas species richness, abundance, and total landscape diversity decline dramatically. Lichen thallus concentrations of N and sulfur (S) also increase or decrease, corresponding to changes in deposition.

10.2.3 Range of Responses Observed

Eastern hardwood forest regions with higher levels of N deposition (US EPA 2002; Table 10.1) exhibit some of the ecosystem responses previously described in this chapter. For example, the long-term reference watershed at the Fernow Experimental Forest, West Virginia, exhibited a 20-year pattern of increasing NO_3^- , Ca^{2+} , and Mg^{2+} export in streamwater; throughfall deposition was $17.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Peterjohn et al. 1996). At the Great Smoky Mountains National Park, export of streamwater N is elevated (Garten 2000, Van Miegroet et al. 2001) at sites within the park receiving deposition of about $32 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Pardo and Duarte 2007, Weathers et al. 2006). In a broad synthesis of data from 354 upland forest catchments across the Northeast, Aber et al. (2003) reported that for catchments receiving less than $8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, surface water NO_3^- concentration rarely exceeded $1 \mu\text{mol L}^{-1}$; above that threshold NO_3^- concentrations in surface water increased. The cross-catchment analysis covered both Eastern Temperate Forests and Northern Forests (Chapter 7). Tree growth response from Wisconsin to Maine and south to Virginia show general increases in net growth and carbon storage as N deposition increases from 3 to $11 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, reflecting an overall fertilization effect of N deposition on eastern and northern forests (Thomas

Table 10.1—Responses to N input for the Eastern Temperate Forests ecoregion

Site	N inputs <i>kg ha⁻¹ yr⁻¹</i>	Response	Comments	Study
New Jersey Pine Barrens	<8	Decreasing ectomycorrhizal fungi morphotype richness		Dighton et al. 2004
North Carolina and West Virginia deposition gradient	>7	Stream NO ₃ ⁻ > DON		Brookshire et al. 2007
Northeastern Forest catchments	8	Surface water NO ₃ ⁻ ≥ 1 μmol L ⁻¹		Aber et al. 2003
Southeastern deposition gradient	9-15	Increasing foliar N concentration		Boggs et al. 2005
North Carolina and West Virginia deposition gradient	<10	Soil C:N <20		Brookshire et al. 2007
Michigan deposition gradient	<12	Arbuscular mycorrhizal fungal biomass decline and community composition change		van Diepen et al. 2008, 2010
Fernow Experimental Forest, WV	<17.5	Herb layer changes		Gilliam et al. 2006a
Fernow Experimental Forest, WV	17.5	Increasing streamwater Ca ²⁺ , Mg ²⁺ , NO ₃ ⁻	Deposition as ambient throughfall	Peterjohn et al. 1996
Cedar Creek LTER, MN	<28	Ectomycorrhizal fungi community response		Avis et al. 2008
Great Smoky Mountains National Park	32	Export of streamwater N		Garten 2000, Pardo and Duarte 2007, Van Miegroet et al. 2001, Weathers et al. 2006
Michigan deposition gradient	<35	Declines in fungal biomass		van Diepen et al. 2007, 2010
Cedar Creek LTER, MN	<50	Ectomycorrhizal fungi community response		Avis et al. 2003

et al. 2010). However, responses vary considerably by species. All hardwood tree species with arbuscular mycorrhizal associations (red maple [*Acer rubrum*], sugar maple, white ash [*Fraxinus americana*], yellow-poplar, and black cherry) as well as six tree species with ectomycorrhizal associations (balsam fir [*Abies balsamea*], pignut hickory [*Carya glabra*], eastern white pine [*Pinus strobus*], quaking aspen [*Populus tremuloides*], northern red and scarlet oak [*Quercus rubra* and *Q. coccinea*]) had marked increases in growth with increasing deposition. In contrast, red pine (*Pinus resinosa*), red spruce (*Picea rubens*), and northern white cedar (*Thuja occidentalis*) all had statistically significant decreases in growth with increasing deposition, and

eight tree species (yellow birch [*Betula alleghaniensis*], eastern white pine, basswood, quaking aspen, bigtooth aspen [*Populus grandidentata*], scarlet oak, chestnut oak [*Quercus prinus*], and northern red oak; all ectomycorrhizal) all had decreased survivorship with increasing deposition. These declines in survivorship could be due to multiple factors, including: direct effects of N itself, spatial covariation between N deposition and exposure to other pollutants (e.g., O₃, SO₄²⁻), N-induced nutrient imbalances, interactions between N loading and secondary stressors such as drought or insect outbreaks, or suppression by competition from other tree species (Thomas et al. 2010).

Table 10.2—Response of Eastern Temperate Forests ecosystems to experimental N fertilization ($\leq 50 \text{ kg ha}^{-1} \text{ yr}^{-1}$)

Site Location	Harvard Forest, Massachusetts		Millbrook, New York	Fernow Forest, West Virginia
Forest Type	Red pine plantation	Black oak & red maple	Chestnut & northern red oak	Mixed central hardwoods
Type of N Deposition	Wet + dry		Wet + dry	Wet + dry
N Deposition <i>kg ha⁻¹ yr⁻¹</i>	9		10	15
N fertilization rate <i>kg ha⁻¹ yr⁻¹</i>	+50		+50 ^b	+35
Form of N Fertilizer	NH ₄ NO ₃		NH ₄ NO ₃	(NH ₄) ₂ SO ₄
Start year	1988		1996	1989
Duration (years)	14		9	11
--Response relative to Control ^a --	Tree growth	0/-	0/+	+
	Mortality	+	0	+
	Foliar %N	+	+	ND
	Foliar %Ca	0	0	ND
	NO ₃ ⁻ leaching	+	0	+
	Cation loss	+	0	+
	Soil C/N	0	0	ND
	N mineralization	0	0	ND
	Nitrification	+	0	ND
	Soil respiration	-		ND
	Microbial biomass	-	-	ND
References	1-6	1-6	7	8-11

^aResponses are indicated as increase (+), decrease (-), or no response (0) in fertilized relative to control plots, or no data (ND) in indicated references.

^bStarted at 100 kg ha⁻¹ yr⁻¹ for 1996-1999, then reduced to 50 kg ha⁻¹ yr⁻¹ thereafter.

References: 1) Magill et al. 2000; 2) Magill et al. 2004; 3) Frey et al. 2004; 4) Bowden et al. 2004; 5) Minocha et al. 2000; 6) Venterea et al. 2004; 7) Wallace et al. 2007; 8) May et al. 2005; 9) Adams et al. 2006; 10) Edwards et al. 2006; 11) DeWalle et al. 2006; 12) Gilliam and Adams 1996.

Experimental N additions indicate broadly similar responses to the gradient studies above (Table 10.2). At the Fernow Experimental Forest, experimental additions of N (35 kg ha⁻¹ yr⁻¹) increased NO₃⁻ leaching (Edwards et al. 2006), decreased soil nutrient cation availability (Gilliam et al. 1996), and decreased tree growth by some species but not others (May et al. 2005, DeWalle et al. 2006). These results resemble those from fertilization experiments at an oak stand at Millbrook, New York (Wallace et al. 2007), and at a red pine stand and an oak-maple stand at Harvard Forest, Massachusetts (Table 10.1; Bowden et al. 2004, Frey et al. 2004, Magill et al. 2000, Magill et al. 2004, Minocha et al. 2000, Venterea et al. 2004). In all but

the oak-maple stand at Harvard Forest, moderate rates of long-term fertilization induced NO₃⁻ leaching, which led to losses of soil base cations. Foliar N content increased at both the red pine and oak-maple stands at Harvard Forest for the duration of that experiment (Magill et al. 2004), whereas the increase in foliar N concentration at the Fernow Experimental Forest was transient in some species (black cherry, red maple) and persistent in others (yellow-poplar; DeWalle et al. 2006, May et al. 2005). These changes in foliar N have had mixed consequences for tree growth. At Harvard Forest, fertilization enhanced growth in the oak-maple stand, but stimulated mortality in the mature red pine stand following a drought in 1995 (Magill et al. 2004). At

Millbrook, New York, chronic N fertilization induced significant mortality in a 60- to 100-year-old chestnut oak/northern red oak stand, but also increased the relative growth rate of the remaining trees, for a net effect of an overall decrease in live basal area in five of six treatment plots after 8 years (Wallace et al. 2007). The most oak mortality occurred at fertilized sites that also had low Ca:Al ratios in surface organic layers (Wallace et al. 2007). At the Fernow Experimental Forest, some tree species (red maple, river birch [*Betula nigra*]) had no response to fertilization, whereas others (black cherry, yellow-poplar) increased growth during the first 7 years, then had decreased growth relative to control trees in years 9 - 12 (DeWalle et al. 2006). Soil processes also often respond to chronic fertilization. Although none of these studies had detectable changes in soil C:N ratio (Magill et al. 2004, Adams et al. 2006), fertilization resulted in higher net nitrification rates at Fernow Forest (Gilliam et al. 2001) and at the Harvard Forest red pine plots (Magill et al. 2000, Venterea et al. 2004). After more than a decade of N addition, both the red pine and the oak-maple stands at the Harvard Forest had decreases in microbial biomass (Frey et al. 2004) and depressed rates of soil respiration relative to the control plot (Bowden et al. 2004).

In a gradient study spanning a range of N deposition rates across North Carolina and Virginia, Boggs et al. (2005) found an increase in foliar N concentration in American beech, sugar maple, and yellow birch as wet N deposition increased from 9 to 15 kg N ha⁻¹ yr⁻¹. Foliar Ca:Al ratios were not affected. Forest floor pH and C:N ratios decreased and rates of net N mineralization and nitrification increased with increasing deposition. In an independent gradient study spanning N deposition rates from 5 to 32 kg N ha⁻¹ yr⁻¹ in North Carolina and West Virginia, Brookshire et al. (2007) found that stream NO₃⁻ and dissolved organic N (DON) concentrations both increased with increasing N deposition, although NO₃⁻ increased most dramatically. Nitrate concentrations exceeded DON concentrations with >7 kg N ha⁻¹ yr⁻¹ of deposition. They also observed a steep decrease in surface soil C:N ratio from 30 to 17 as deposition increased from 5 to 10 kg N ha⁻¹ yr⁻¹, after which soil C:N ratio did not decrease further with increasing deposition.

The impact of excess N via acidification was assessed by both Fox et al. (1989) and Adams et al. (1991) using a “Green-Yellow-Red” screening model to determine levels of acid deposition (N and S) that would impact Class 1 wilderness areas. At the green line value, vegetation health and vigor would be protected; at the red line value, changes in N cycling, species composition, or other ecosystem features could occur (Fox et al. 1989). For Joyce Kilmer, North Carolina, and Slick Rock, Tennessee, the green line value for total N deposition was 7 to 10 kg N ha⁻¹ yr⁻¹; damage would occur at 15 kg N ha⁻¹ yr⁻¹ (red line). In Otter Creek, West Virginia, the green line value was 7 kg N ha⁻¹ yr⁻¹; the red line value was 10 to 15 kg N ha⁻¹ yr⁻¹ (Fox et al. 1989). Adams et al. (1991) used the same approach to determine N and S deposition levels that would prevent foliar injury and fish species shifts. They set green line values of 5 to 8 kg N ha⁻¹ yr⁻¹ for Dolly Sods, West Virginia; Hercules Glade, Missouri; and Otter Creek, West Virginia. Significant ecosystem damage could be expected at total N deposition level >20 kg N ha⁻¹ yr⁻¹ (Adams et al. 1991).

Herbaceous layer. Responses of the herb layer to excess N vary among temperate deciduous forest sites. A northern forest (Adirondack) ecosystem had large shifts in herb cover in response to modest N additions (Hurd et al. 1998). At the Watershed Acidification Study at Fernow Experimental Forest, West Virginia, which has ambient deposition of approximately 17.5 kg N ha⁻¹ yr⁻¹ in throughfall (Adams et al. 1993), addition of 35 kg N ha⁻¹ yr⁻¹ via aerial application has led to changes in herbaceous species composition. Recently, similar changes in herbaceous species composition have been observed over time on the adjacent reference (control) watershed, which receives only atmospheric deposition⁹. Previous research (Gilliam et al. 2006a) at the same watershed had shown no significant differences in herb cover, composition, or several diversity indicators between treatment and control watersheds for any of the years sampled (1991, 1992, and 1994). Gilliam et al. (2006a) suggested that the initial lack of observed

⁹Gilliam, F.S. Unpublished data. Professor, Department of Biological Sciences, Marshall University, Huntington, WV 25755-2510.

response to N addition was due to high background levels of N deposition that had already saturated watershed soils. Because the ecosystem had already been altered by N inputs, changes in the herb layer had already occurred. This is consistent with the conclusion of Hurd et al. (1998) that sensitivity of the herb layer to N additions was largely a function of ambient N deposition.

Ectomycorrhizal fungi. Ectomycorrhizal fungi form associations with many of the dominant trees of drier or nutrient-poor sites in the region, including oak, hickory, beech, birch, and basswood (*Quercus*, *Carya*, *Fagus*, *Betula*, *Tilia*). There has been less research on ectomycorrhizal response to N deposition in hardwood than in conifer forests. We expect hardwood forest types that have a strong ecological overlap with conifer forest types of this region (e.g., oligotrophic beech-dominated northern hardwoods and oligotrophic oak forests) to have similar community responses to N deposition, but at this time, this supposition is unsupported by data. In an oak savannah forest in east-central Minnesota, ectomycorrhizal fungal community response (reduced species richness of sporocarps, changes in communities seen on root tips and sporocarps) was seen with addition of 50 and 170 kg ha⁻¹ yr⁻¹ over 18 to 20 years (Avis et al. 2003). The treatments also involved fertilization with other nutrients, so are not strictly equivalent to N deposition. In an N-only fertilization experiment Avis et al. (2008) also found a change in oak forest ectomycorrhizal fungal communities with deposition plus additions of N of approximately 28 kg N ha⁻¹ yr⁻¹. However, we do not know the lower threshold for this response. Studies of other ectomycorrhizal community types (e.g., *Betulaceae*, *Salicaceae*) are lacking.

Arbuscular mycorrhizal fungi. Arbuscular mycorrhizal fungi form associations with many tree taxa dominant in this forest type, including maple, ash, yellow-poplar, sweet gum, and cherry (*Acer*, *Fraxinus*, *Liriodendron*, *Liquidambar*, and *Prunus*). We have very little empirical data on arbuscular mycorrhizal community response to N in forests. One study in sugar maple dominated forests in Michigan has found declines of arbuscular mycorrhizal fungal biomass and change in community composition in response to addition of 30 kg⁻¹ ha⁻¹

yr⁻¹ over and above background deposition across a gradient ranging from approximately 5 to 12 kg ha⁻¹ yr⁻¹ wet deposition (van Diepen et al. 2007, 2010; van Diepen 2008). There is some indication that arbuscular mycorrhizal biomass has declined and community composition has shifted over the N deposition gradient (van Diepen et al. 2007, 2010; van Diepen 2008), suggesting a threshold of <12 kg ha⁻¹ yr⁻¹ of wet deposition, but it is likely that there are interactions with within-site factors, and definitive determination of a response threshold awaits further analysis.

Lichens. Air pollution has been a major factor in the depauperization of the lichen flora in the eastern hardwoods region during the past 100 years (e.g., see Murphy et al. (1999; Massachusetts), Smiley and George (1974; New York), Showman and Long (1992; Pennsylvania); Wetmore (1989) and Showman (1975; Ohio); Wetmore (1988) and McCune (1988; Indiana and Michigan); or Lawrey and Hale (1988; Virginia)). Historically, the most damaging pollutants have been SO₂, sulfuric acid (H₂SO₄), nitrogen oxides (NO_x), and nitric acid (HNO₃). As an example, declines in lichen species diversity exceeding 80 percent in Cuyahoga National Park (Ohio) and Indiana Dunes National Lake Shore, between 1895 and 1988, were attributed to SO₂ (Wetmore 1988, 1989). Nutrient N, especially in the form of ammonium (NH₄⁺), is a newly recognized concern.

It is entirely possible that a widespread modification of native lichen flora has taken place across the eastern forests due to air pollution and habitat loss. In 2007, after substantial, regionwide decreases in SO₂ and NO_x emissions, total wet N deposition was still 2 to 5 times higher throughout the eastern hardwoods ecoregion compared to background western U.S. localities. In some regions, NH₄⁺ is a significant portion of deposition (NADP 2009). Although species richness remains high in parts of the southern Appalachians and southeastern Georgia (McCune et al. 1997), north central Florida (DeBolt et al. 2007), and Maine (Hinds and Hinds 1998), the paucity of historical records complicates confirmation of intact lichen community composition, species richness, cover, and/or landscape-level diversity in most locations.

Table 10.3—Previously determined critical loads of nutrient N for the Eastern Temperate Forests ecoregion

Site	Critical load for nutrient N <i>kg N ha⁻¹ yr⁻¹</i>	Comments	Study
Great Smoky Mountains National Park	3-7	Determined using steady state mass balance method	Pardo and Duarte 2007
Great Smoky Mountains National Park	2.5-9	Determined using steady state mass balance method	Oja and Arp 1998

Declines in SO₂ and NO_x emissions in response to the Clean Air Act have been linked to improvements in epiphytic lichen diversity and cover in the upper Ohio Valley (Showman 1981, 1990, 1998) and south central Pennsylvania (McClenahan et al. 2007) and lower tissue S concentrations in Virginia (Lawrey and Hale 1988). For the Ohio and Pennsylvania study areas, 2007 total wet N deposition was still between 6.2 and 7.2 kg N ha⁻¹ yr⁻¹ in 2007 (NADP 2009). As a result, the returning species are moderately acid- and SO₂-sensitive, but N tolerant (Geiser et al. 2010). This response is consistent with substantial regional decreases in acidity but increasing N in wet deposition between 1980 and 2007 (NADP 2009).

More information on lichen research methodology and terminology can be found in Chapter 4 of this volume.

10.2.4 Critical Loads Estimates

The critical load for decreased tree growth and survivorship in response to N deposition is >3 kg N ha⁻¹ yr⁻¹, while the critical load for herbaceous species is <17.5 kg N ha⁻¹ yr⁻¹. Empirical critical loads for nutrient N in eastern hardwood forest ecosystems can be set at 8 kg N ha⁻¹ yr⁻¹ for NO₃⁻ leaching (Table 10.5). This threshold applies for surface water NO₃⁻ leaching in the northeastern United States (Aber et al. 2003), as well as for select forests in the southeastern United States, where Brookshire et al. (2007) observed stream NO₃⁻ concentrations to exceed those of dissolved organic N above 7 kg N ha⁻¹ yr⁻¹. Similarly, Lewis (2002) used 10 kg N ha⁻¹ yr⁻¹ as a deposition criterion for “minimally disturbed” watersheds in a compilation of N yield from watersheds across the United States.

Critical loads for nutrient N calculated using the steady-state mass balance method (Pardo 2010, UBA 2004) were reported (Table 10.3) for Great Smoky Mountains National Park as ranging from 3 to 7 kg ha⁻¹ yr⁻¹ (Pardo and Duarte 2007). Earlier calculations of critical loads for N nutrient within Great Smoky Mountains National Park made using data from the Integrated Forest Study (Johnson and Lindberg 1992) ranged from 2.5 to 9 kg N ha⁻¹ yr⁻¹ (Oja and Arp 1998).

Critical loads for ectomycorrhizal fungi, arbuscular mycorrhizal fungi, and lichens have not been reported previously. The critical load for ectomycorrhizal fungi is expected to be much less than the N input level of 28 kg ha⁻¹ yr⁻¹ reported by Avis et al. (2008); the critical load for arbuscular mycorrhizal fungi is also expected to be less than the 35 kg ha⁻¹ yr⁻¹ that caused a mycorrhizal response in research by van Diepen et al. (2007), and may be less than 12 kg N ha⁻¹ yr⁻¹ (van Diepen 2008). Arbuscular mycorrhizal fungal critical loads are tentatively set at <12 kg N ha⁻¹ yr⁻¹ (van Diepen 2008). The value for arbuscular mycorrhizal fungi is considered expert judgment, as it is based on one gradient with only four sites.

Lichen community-based critical loads are difficult to pinpoint in the eastern hardwoods region due to the confounding effect of acidity from sulfur-containing pollutants, habitat alterations, and changing climate. However, N critical loads are probably similar to those proposed for epiphytic macrolichens in other temperate forests of the United States (northwest forested mountains (3.1 to 5.2 kg N ha⁻¹ yr⁻¹), west coast marine forests (2.7 to 9.2 kg N ha⁻¹ yr⁻¹), Mediterranean

Table 10.4—Previously determined critical loads of acidity for the Eastern Temperate Forests ecoregion

Site	Critical load for N acidity $kg\ N\ ha^{-1}\ yr^{-1}$	Response	Study
Joyce Kilmer, NC; Slick Rock, TN	7-10	Vegetation health and vigor	Fox et al. 1989
Otter Creek, WV	7	Vegetation health and vigor	Fox et al. 1989
Otter Creek, WV; Hercules Glade, MO; Dolly Sods, WV	5-8	ANC = 25	Adams et al. 1991

California (3.3 to $5.5\ kg\ N\ ha^{-1}\ yr^{-1}$)), due to species overlap and physiological/ecological similarities among epiphytic macrolichens. Application of the western Oregon and Washington model relating epiphytic lichen community composition to N deposition (Chapter 4, Geiser et al. 2010), to eastern hardwoods yields a critical load estimate of 4 to $8\ kg\ N\ ha^{-1}\ yr^{-1}$. This value was calculated using a precipitation range of 71 to $305\ cm$, and a lichen community-composition response threshold that allows as few as 25 percent oligotrophs and no more than 47 percent eutrophs. This response threshold is higher than that used for Oregon and Washington to allow for the higher nutrient content of leaf exudates and more neutral bark substrates in hardwood forests, which favor eutrophs. (Coniferous forests predominate in western Oregon and Washington.)

A number of estimates of critical loads for acidity have also been set for the region and are summarized in Table 10.4. Critical loads for N associated with acidity often tend to be higher than those for nutrient N; for this ecoregion, they were of similar magnitude. The red line/green line approach of Fox et al. (1989) has been used to establish critical loads for acidity for eastern forests. Using the green line value determined for Joyce Kilmer, North Carolina, the critical load for acidity for the overstory and herb layer was $7\ kg\ N\ ha^{-1}\ yr^{-1}$. This is consistent with calculations made for this region by McNulty et al. (2007), who made coarse estimates for critical loads for total acidity across the United States. Based on those calculations, the contribution of N to those critical loads for acidity is $\sim 10\ kg\ ha^{-1}\ yr^{-1}$. Earlier

assessments in this region suggest that the critical load for acidity has been exceeded for both terrestrial and aquatic ecosystems (Fox et al. 1989, Sullivan and Cosby 2002, Sullivan and Cosby 2004, Sullivan et al. 2003).

10.2.5 Comparison to European Critical Loads

These estimates for critical loads are somewhat lower than for comparable ecosystems in Europe. Critical loads for European deciduous forests are set at 10 to $15\ kg\ N\ ha^{-1}\ yr^{-1}$ for increased NO_3^- leaching and increased N mineralization and nitrification; at 15 to $20\ kg\ N\ ha^{-1}\ yr^{-1}$ for alterations in tissue chemistry and increased susceptibility to pest outbreak; and at 10 to $20\ kg\ N\ ha^{-1}\ yr^{-1}$ for alterations in mycorrhizal community composition (UBA 2004). In a review and synthesis on effects of atmospheric ammonia (NH_3) on terrestrial vegetation that included critical load estimates, Krupa (2003) reported a critical load range of 15 to $20\ kg\ N\ ha^{-1}\ yr^{-1}$ for deciduous forests of Europe.

Herbaceous layer. Critical loads for ground vegetation in temperate forests are set at 10 to $15\ kg\ N\ ha^{-1}\ yr^{-1}$ in Europe (UBA 2004). Critical loads research in Europe often employs gradients in N deposition (Brunet et al. 1998, Strengbom et al. 2003). Most such work is done in conifer forests of Europe, limiting direct comparisons to the herb layer of temperate deciduous forests in the eastern United States. Brunet et al. (1998) employed multivariate methods to assess potential effects of N deposition on herb layer species of oak forests by sampling along a gradient of N deposition in southern Sweden. Species that increased in cover with increased N deposition were generally both nitrophilous and acid

Table 10.5—Empirical critical loads of nutrient N for the Eastern Temperate Forests ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem	Ecosystem component	Critical load for nutrient N kg N ha ⁻¹ yr ⁻¹	Reliability	Response	Comments	Study
Eastern hardwood forests	Trees	>3	#	Decreased growth of northern white cedar, and decreased survivorship of yellow birch, scarlet and chestnut oak, quaking aspen, and basswood		Thomas et al. 2010
Eastern hardwood forests	Lichens	4-8	(#)	Changes in epiphytic lichen community composition		Geiser et al. 2010
Eastern hardwood forests	Forests	8	##	Increased surface water loading of NO ₃		Aber et al. 2003
Eastern hardwood forests	Arbuscular mycorrhizal fungi	<12	(#)	Arbuscular mycorrhizal fungal biomass decline and community composition change	Observed along a Michigan N gradient	van Diepen 2008
Eastern hardwood forests	Herbs	<17.5	(#)	Herb layer changes	Observed at Fernow Experimental Forest, WV	Gilliam 2006, 2007, Gilliam et al. 2006a
Southeastern Coastal Plain	Lichens	4-6	(#)	Changes in epiphytic lichen community composition		Application of Geiser et al. 2010
Southeastern Coastal Plain	Ectomycorrhizal fungi	5-10	(#)	Ectomycorrhizal fungi community response		Dighton et al. 2004; Lilleskov et al. 2001, 2002, 2008

tolerant. They concluded that N deposition influenced vegetation directly by increasing N availability and indirectly by increasing soil acidity.

10.2.6 Future Research Directions and Gaps in Data

Research on critical loads for eastern hardwood forests of the United States lags far behind research for similar forests in Europe. Particularly lacking are empirical data on community responses to gradients of ambient N deposition. Plot-scale fertilizer studies have been conducted, but these are not as numerous as similar studies in Europe, and carry with them the inherent difficulty of scaling up from the plot to the landscape scale. Studies that employ whole-watershed treatment with N, such as that at Fernow Experimental Forest, are extremely rare. Additional complexities affecting responses to N loading include interactions between N addition and climate events (disturbance and variation), prior land use, species composition, site characteristics, and hydrology. For example, the coincidence of increased N availability, drought, and soil nutrient cation depletion appear to have led to significant tree mortality at sites in Massachusetts (Magill et al. 2004) and eastern New York (Wallace et al. 2007), suggesting that the incipient N saturation at the site made the trees more susceptible to secondary stresses. Multi-factor experimental manipulations that addressed N interactions with climate and other stressors could help address some of these uncertainties.

Also useful would be more studies focusing on gradients in N deposition (e.g., Boggs et al. 2005, Brookshire et al. 2007) and on forests of varying stand age (Castro et al. 2007). Gradient studies would be especially useful in filling the large data gaps that exist on the response of mycorrhizal fungal communities to realistic levels of N deposition in this region, especially in the development of response functions to N deposition that would permit establishment of critical loads.

A framework grid system has been systematically surveyed for lichens in New England and Mid-Atlantic states (Maine through Virginia) by the U.S. Forest Service Forest Inventory and Analysis/Forest Health Monitoring (FIA/FHM) program (McCune 2000, Will-

Wolf et al. 2006); matching deposition estimates and supplementary sites are needed to interpret these data to estimate critical loads. Despite major reductions in SO_2 and NO_x , critical loads for nutrient N for epiphytic lichens are probably still exceeded in much of the region. Lichen floras dating back to about 1900, where available, would help elucidate the changes that have already taken place. Research is also needed to separate H_2SO_4 and HNO_3 acidification effects from fertilizing N effects on lichen community composition, diversity, and physiology, with consideration to the influences of habitat alteration and climatic changes. Forests of Minnesota and Wisconsin, where hydrogen ion (H^+) and SO_4^- deposition are close to background levels but NO_3^- and NH_4^+ deposition are elevated, may offer an opportunity for such studies when compared to forests of Ohio, Pennsylvania, West Virginia, and New York with high acidity, S deposition, and N deposition.

10.3 Southeastern Coastal Plain

10.3.1 Ecosystem Description

Forest ecosystems of the Southeastern Coastal Plain have evolved under conditions of relatively high frequency of fire and hurricanes (Gilliam et al. 2006b). The forests of the coastal plain contrast with other forest types in the Eastern Temperate Forests ecoregion in that: (1) coastal plain forests tend to comprise pine-dominated overstories of low biodiversity and herb-dominated understories often of very high biodiversity (Gilliam 2007, Platt et al. 2006); and (2) coastal plain forests experience lower levels of atmospheric deposition of N.

10.3.2 Ecosystem Responses to N Deposition

Coastal Plain forest responses to N deposition are not well studied. Generally, we would expect the same responses to excess N as seen in eastern hardwood forests: increases in tissue N concentration, declines in biodiversity, shifts in soil N cycling and NO_3^- leaching, decreases in soil C:N ratio, and shifts in community composition (section 10.2.2). Interactions of N deposition with ecosystem processes in the Southeastern Coastal Plain are complicated by a changing N deposition regime, spatially variable fire dynamics, and disturbances caused by large tropical storms. Historically, many pine-dominated forests of the Coastal

Plain have been fire maintained. Fire varies in frequency throughout the region and alters the N status of the ecosystem (Boerner et al. 2004). In a meta-analysis, Wan et al. (2001) found that fire invariably caused substantial loss of N from fuels (i.e., forest litter). For example, as much as 50 percent of litter N was lost in a single fire for conifer forests.

Tropical storms are an important disturbance regime in forest ecosystems of the coastal plain (Gilliam et al. 2006b). These disturbances can have a substantial impact of nutrient cycling in these ecosystems. It is possible that the frequency/intensity of tropical storms is increasing as a result of global warming.

10.3.3 Range of Responses Observed

Although the effect of S deposition on coastal plain ecosystems has been studied (Janicki et al. 1995), little research has been done on responses of the coastal plain ecosystem to excess N deposition.

Ectomycorrhizal fungi. One study in the Pine Barrens region of New Jersey found a trend of decreasing morphotype richness with increasing N deposition (Dighton et al. 2004). There was significantly lower mycorrhizal morphotype richness at a site with bulk deposition of $8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ than at a site with approximately $4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Dighton et al. 2004). Low number of sample points in the gradient weakens the evidence for causal linkages, but this evidence is consistent with that from other oligotrophic conifer-dominated ecosystems that suggest thresholds of somewhere between 5 and $10 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for community response (Lilleskov et al. 2001, 2002, 2008). More productive pine or deciduous ecosystems in the southern part of this ecosystem type, on richer soils or with significant N removals via harvest and/or fire, might have a higher deposition threshold. However, no data are available from the region with which to test this hypothesis.

Lichens. Acidifying and fertilizing pollutants in deposition (N and S), primarily from urban/industrial emissions, have strongly influenced lichen communities in the Southeastern Coastal Plain. The characteristic

response has been loss of sensitive species resulting in sharply reduced species richness and reduced lichen cover. For example, even by 1966, epiphytic lichen diversity was low (14 species per plot) on the north shore of Long Island, up to 62 km from Brooklyn (New York City; Brodo 1966). There was complete extirpation of all lichens within 19 km of Brooklyn's industrial center, even though Brooklyn and the north shore of Long Island shared the same flora historically (Brodo 1966). Of 70 species detected around 1900 on Plummer's Island, a protected habitat 15 km south of Washington, D.C., only 20 could be found in the early 1990s (Lawrey 1993). Such extreme de-pauperization of the lichen flora is less pervasive in the southeastern states. In an analysis of FIA/FHM epiphytic macrolichen data from forests of Georgia, the Carolinas, eastern Tennessee, and Virginia, McCune et al. (1997) observed pollution-tolerant species and lower species richness in urban and industrial areas, but pollution-sensitive and 'luxuriant and diverse' lichens (up to 40 species per plot) in many rural areas. The richer flora is consistent with generally lower deposition of S and N in states of the southeastern compared to the northeastern United States. However, lacking historic flora, it is not possible to confirm whether species are missing from communities in the southeast that are experiencing lower S and N deposition. Some aspects of the flora hint at a widespread loss of species due to air pollution: only one fruticose genus was detected and cyanolichens were rare.

Fire has less influence on the N regimes of forest lichens compared to soil-rooted plants in the Southeastern Coastal Plain. Lichens that are not consumed or heat-killed during forest fire become a propagule source for recolonization without long term shifts in community composition (Johansson et al. 2006, Sillet and Goslin 1997). However, increased fire frequency and short timber harvest cycles favors faster growing species over those with greater dispersal or growth rate limitations, shifting community composition and reducing diversity (DeBolt et al. 2007).

More information on lichen research methodology and terminology can be found in Chapter 4 of this volume.

10.3.4 Critical Loads Estimates

Until more research has been done in Southeastern Coastal Plain forests, we can only offer provisional critical loads. Our best estimate of the critical load for ectomycorrhizal community integrity is 5 to 10 kg N ha⁻¹ yr⁻¹, and even this must be regarded as highly uncertain and only applicable to low productivity pine barrens forests (Table 10.5). In other ecosystem types, critical loads for mycorrhizal fungi appear to be roughly equivalent to those for other receptors, but definitive characterization of critical loads for other receptors and responses awaits further research.

Application of the western Oregon and Washington model relating epiphytic lichen community composition to N deposition (Chapter 4, Geiser et al. 2010) to Southeastern Coastal Plains yields a critical load estimate of 4 to 6 kg ha⁻¹ yr⁻¹. This value was calculated using a precipitation range of 102 to 178 cm, and a lichen community-composition response threshold that allows as few as 30 percent oligotrophs and no more than 34 percent eutrophs. This response threshold represents the upper end of the response threshold range used for Oregon and Washington to allow for potential favoring of the mesotrophs and eutrophs by warmer temperature. These species are generally more drought resistant than oligotrophs.

10.3.5 Comparison to European Critical Loads

The concept of critical loads for N was originally developed for forest ecosystems of Europe (Nilsson and Grennfelt 1988). Whereas most of these forests have long been altered by human use (Dambrine et al. 2007), they generally do not experience frequent natural disturbances, such as fire and extreme wind events. Thus, it is difficult to compare Southeastern Coastal Plain ecosystems to European ecosystems.

10.3.6 Future Research Directions and Gaps in Data

More research is needed on the effects of N deposition to ecosystems of the Southeastern Coastal Plain. Potential research areas include watershed and plot scale fertilization studies and deposition gradient studies. In addition, research should be conducted to examine how the interaction of frequent disturbance and N

deposition affect the N status of the Coastal Plain. Research is also needed to separate H₂SO₄ and HNO₃ acidification effects from fertilizing N effects on lichen community composition, diversity, and physiology, with consideration to the influences of habitat alteration, climatic changes and changes in fire frequency. Southern Georgia and north-central Florida, with the lowest N and S deposition, may be good locations for field-based N addition studies.

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