16 TROPICAL AND SUBTROPICAL HUMID FORESTS

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16.1 Ecoregion Description

Tropical humid forests of the United States are located below 1000 m in elevation and experience average year-round temperatures between 20 °C to 26 °C, receive more than 1500 mm of precipitation annually, and experience fewer than three dry months per year (CEC 1997; Fig. 2.2). In addition to tropical humid forests, we include in this chapter lower montane and low elevation tropical and subtropical humid forests with precipitation >1000 mm and mean annual temperatures >16 to 20 °C. Regions within the United States that contain forests of this type include coastal, low elevation, and lower montane regions: (1) on the windward slopes of the Hawaiian Islands, and (2) across Puerto Rico. Additionally, included in this chapter are (3) forests of the coastal plains of southern Florida within the greater Everglades wetland ecosystem, although mangrove and other saturated or seasonally saturated ecosystems are biogeochemically quite distinct and thus may respond differently than other, upland tropical forests discussed in this chapter. Tropical and subtropical humid forests occur in warm climates with plentiful rainfall and are thus well suited for agriculture. Consequently, many of the remaining forests of this type in the United States are in various stages of recovery following agricultural abandonment and are composed of a mix of native and exotic species. Native or primary forests in this class are highly fragmented and threatened by anthropogenic changes in land use and hydrology, and by invasive species. However, protected areas that contain forest communities less impacted by human activity compared to surrounding areas occur within each of the three regions. Some of the largest protected areas of tropical and subtropical forests in the United States include Hawai'i Volcanoes and Haleakala National Parks and a suite of forest reserves in the Hawaiian Islands; El Yunque National Forest in Puerto Rico; mangroves, tropical hammocks, and other tree islands within the Everglades and Biscayne National Parks; and protected pineland preserves in Dade and Monroe Counties, southern Florida.

16.1.1 Subtropical Humid Forests of Hawaii: Ecosystem Description

Subtropical humid forests in Hawaii are diverse, varying with rainfall and elevation, time since disturbance, degree of invasion, topography, and soil age. Native forest communities include the common dominant trees ohi'a lehua (*Metrosideros polymorpha*) and koa (*Acacia koa*), tree ferns, other common wet forest tree species (e.g., ʻōlapa [*Cheirodendron* spp.]) and Hawaiian holly (*Ilex anomala*), and a diverse understory of epiphytes and shrubs. Rates of endemism in the Hawaiian Islands are among the highest in the world, in part due to their isolated geography. Notable among these communities is a diversity of endemic birds and lobelioids, which are a special group of flowering plants in the Campanulaceae (bellflower) family. Few, purely native Hawaiian wet forest communities exist at low elevations but instead consist of a mix of native and exotic species (Zimmerman et al. 2008). However, at higher elevations, tracts of intact humid forest remain in protected areas on most islands (Ricketts et al. 1999).

16.1.2 Subtropical Humid Forests of Puerto Rico: Ecosystem Description

Subtropical humid forests of Puerto Rico are also diverse biologically and geographically, occurring primarily as secondary growth in former agricultural or pasture lands or as primary or successional growth within remnant, protected forest reserves. These ecosystems are composed of various plant communities that are associated with gradients in tidal inundation, rainfall, elevation, soil characteristics determined by geology, and time since disturbance (e.g., human, landslides, hurricanes) (Ewel and Whitmore 1973). Subtropical wet forests on volcanic soils include tabonuco forest at lower elevations in various stages of succession, dominated by abundant epiphytes and the tabonuco tree (*Dacryodes excelsa*) among others. Colorado and dwarf cloud forests grow at higher elevations, associated with trees such as palo colorado (*Cyrilla racemiflora*) and nemoca cimarrona (*Ocotea spathulata*), respectively. Forests on serpentine

or limestone-derived soils are more xerophytic, supporting sclerophyllous, evergreen vegetation (Ewel and Whitmore 1973). Subtropical forests on the humid northern and southern coasts of Puerto Rico contain mixed stands of red, black, and white mangroves (*Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*) (Tomlinson 1986).

16.1.3 Tropical Forests of Southern Florida: Ecosystem Description

Tropical forests in southern Florida include pine rocklands and hardwood hammocks in the uplands, various 'tree islands' that are surrounded by occasional or persistent water, and coastal mangrove communities. Florida pine rocklands and tropical hardwood hammocks are located on shallow soils of limestone outcroppings in higher elevations of the Everglades (Lodge 2004). Pineland ecosystems are fire-maintained, dominated by Florida slash pine (*Pinus elliottii*) and saw palmetto (*Serenoa repens*). Tropical hardwood hammocks develop in the absence of fire, and are composed of numerous species characteristic of the Caribbean such as gumbo limbo (*Bursera simarouba*) and mahogany (*Swietenia mahogani*). Pinelands and hardwood hammocks are highly threatened by urbanization and land-use change, composing 2 percent of their former range (Ricketts et al. 1999). Mangroves are extensive along the southern Florida coastline, providing habitat for a variety of marine, estuarine, and terrestrial species of mammals, birds, reptiles, invertebrates, and fish. These forests are dominated by red, black, and white mangroves, and buttonwood (*Conocarpus erectus*). Various other tree islands exist in the Everglades ecosystem, maintained by seasonal hydroperiods and serving as biogeochemical and floral hotspots on the flooded landscape (Sklar and van der Walk 2002). Common species within tree islands in the Everglades include the strangler fig (*Ficus aurea*) and coco plum (*Chrysobalanus icaco)*, among others (Wetzel et al. 2008).

16.2 Ecosystem Responses to N Deposition

Few studies have explored the impacts of nitrogen (N) enrichment on ecological processes in tropical and subtropical humid forests worldwide, and none have explicitly assessed the consequences of atmospheric N deposition in the three tropical ecoregions of the United States. However, exceptional, long-term N addition experiments within native ecosystems of Florida and Hawaii have contributed greatly to our understanding of tropical forest functioning (Table 16.1; Feller et al. 2007, 2009; Vitousek 2004). Existing studies used high rates of fertilizer addition primarily to assess nutrient limitation of vegetation and thus are not useful in identifying thresholds of response to N inputs. Nonetheless, these fertilization experiments and others do suggest that plant growth and ecosystem processes in some humid tropical and subtropical forests may be susceptible to N enrichment while others may be less susceptible, depending on numerous factors that alter forest nutrient status.

In the following sections we summarize the types and range of ecosystem responses to N fertilization observed in native U.S. tropical and subtropical forests. However, because the consequences of N deposition have not been well studied in these regions, evidence is also included from fertilization studies in other tropical forests that may operate similarly to those in Hawaii, Puerto Rico, and southern Florida. Data from non-U.S. forests are used only as supporting evidence; thus, information in this chapter is not intended to be a thorough review of ecosystem responses to N deposition or fertilization in tropical/subtropical forests worldwide. Information from non-U.S. regions is noted where included.

Nutrient limitation of primary production cannot be assessed using indirect measures of ecosystem N availability or cycling (Tanner et al. 1998). However, without abundant data, we broadly characterize tropical forests as relatively 'N-rich' or 'N-poor' and summarize the responses observed in these systems following N fertilization or those expected following N deposition.

In N-rich tropical and subtropical forests where primary production or nutrient cycling may be limited by factors other than N, N enrichment is not expected to change plant growth or species composition, although some evidence suggests that tissue chemistry, decomposition, and herbivory may be altered in some ecosystems (Benner and Vitousek 2007, Feller et al. 2007, Ostertag

Table 16.1—Responses to long-term N-fertilization of native tropical and subtropical humid forests of the United States and related ecosystems.[a]

Site Location	Hawaii, Lower montane forests		Florida and Belize, Coastal mangrove forests	
Forest Type	N-limited, *M. polymorpha* (ohi'a lehua)	P-limited, *M. polymorpha* (ohi'a lehua)	N-limited, Florida	P-limited, Belize
Type of N Deposition	Wet, dry, fog	Wet	Wet	Wet + dry
N Deposition kg ha^{-1} yr^{-1}	17	< 1	4	2
N Fert. Rate kg ha^{-1} yr^{-1}	100	100	>100	>100
Form of N Fertilizer	Urea/NH_4NO_3	Urea/NH_4NO_3	Urea	Urea
Start year	1985	1991	1997	1997
Duration (years)	11-13	5-7	2-4	2-4
--Response relative to Control [b]--				
Tree growth	+	0	+	0
Foliar %N	+/0	+	+	0
Herbivory	ND	ND	+	-
Plant community composition	+	0	ND	ND
Epiphyte abundance	ND	0	ND	ND
Decomposition	0	+	ND	ND
Soil C:N	0	0	ND	ND
N mineralization	+	+	ND	ND
Nitrification	+	+	ND	ND
Microbial biomass N	0	0	ND	ND
N-oxide emissions	+	+	ND	ND
NO_3^- leaching	+	+	ND	ND
Soil pH	0	0	0	0
References	1-7	1-8	9-11	11,12

[a] Studies from Belize included to illustrate differences in ecosystem response to N fertilization in N-limited (Florida) vs. P-limited mangrove ecosystems.

[b] Responses are indicated as increase (+), decrease (–), or no response (0) in fertilized relative to control plots, or no data (ND) in indicated references.

References: 1) Vitousek et al. 1993; 2) Harrington et al. 2001; 3) Ostertag and Hobbie 1999; 4) Lohse and Matson 2005; 5) Hall and Matson 2003; 6) Ostertag and Verville 2002; 7) Cordell et al. 2001; 8) Benner et al. 2007; 9) Caccia and Boyer 2007; 10) Feller et al. 2003a; 11) Feller et al. 2007; 12) Howarth et al. 1996.

and Hobbie 1999, Ostertag and Verville 2002). On the other hand, N addition to N-rich tropical forests may immediately increase N losses as gases (NO_x, N_2O, or N_2) or in drainage, but this response depends in large part on soil properties, redox conditions, and hydrological pathways (Hall and Matson 2003, Herbert and Fownes 1995, Lohse and Matson 2005, Templer et al. 2008). Rivers that drain N deposition-affected tropical forests may experience increases in nitrate (NO_3^-) relative to dissolved organic N, which is the form of N that typically dominates export of undisturbed tropical catchments (Downing et al. 1999, Lewis et al. 1999; reviewing tropical forests in the Americas and worldwide).

In tropical and subtropical forests where N availability is relatively low, ecosystem responses to atmospheric N deposition are expected to be similar to temperate forests and include increased plant growth, elevated rates of soil N cycling, increased foliar N concentration

Table 16.2—Empirical critical loads of nutrient N for the Tropical and Subtropical Humid Forests ecoregion. Reliability rating: (#) – expert judgment; no data are available for this ecosystem category. The critical load is based on expert judgment and knowledge of ecosystems which may function similarly.

Ecosystem component	Critical load for N deposition *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
N-poor tropical and subtropical forests	5-10	(#)	Changes in community composition; NO_3^- leaching, N trace gas emissions	Critical load for N-poor forests based on estimates for Southeastern Coastal Plain forests	ND
N-rich tropical and subtropical forests	<5-10	(#)	NO_3^- leaching, N trace gas emissions	Critical load for N-rich forests should be lower than for N-poor forests based on possibility of N losses	ND

and herbivory of some plant species, possible changes in community composition, and eventually elevated N losses as NO_3^- or as gases as ecosystems become N saturated (Erickson et al. 2001, Feller et al. 2007, Hall and Matson 2003, Lohse and Matson 2005, Ostertag and Verville 2002, Vitousek and Farrington 1997). However, unlike in some temperate forests, atmospheric N deposition may be retained first in the canopy rather than the forest floor (Wanek et al. 2007), for example, stimulating nutrient cycling and growth within epiphyte communities that intercept cloud and rainwater (Clark et al. 2005, Reich et al. 2003; both in Costa Rica).

Alkaline soils in Puerto Rico and southern Florida can be expected to have high acid neutralizing capacity that may buffer acidity derived from N deposition. In contrast, highly weathered, poorly buffered volcanic soils in Puerto Rico and Hawaii or peat soils in Florida may be more susceptible to the negative effects of acidity, including elevated aluminum mobility and phosphorus (P) fixation in soils that can further limit primary production (Asner et al. 2001; Matson et al. 1999, 2002; all review tropical forests worldwide). Alkaline sea salt aerosols and dust likely enter coastal tropical forests but it is unclear whether these inputs will mitigate the impacts of acidity generated from deposition and microbial N cycling in soils (Evans et al. 2004 for Florida; Vogt et al. 2007 for a review of tropical forests worldwide).

16.3 Range of Responses Observed

Although small in their geographical extent within the United States, tropical and subtropical humid forests harbor an extraordinary diversity of soil types, species, plant assemblages, landscape characteristics, and landscape histories that will likely vary in their sensitivity to N enrichment (Nardoto et al. 2008 in Brazil; Townsend et al. 2008 for tropical forests worldwide). Furthermore, few studies have tested nutrient limitation of plant growth in tropical or subtropical forests or have explored soil and microbial responses to N additions in these regions, further compounding the uncertainty about how these forests will respond to N deposition.

16.3.1 N-Rich Tropical and Subtropical Forests

Worldwide, many tropical and subtropical forests are rich in N relative to other limiting factors, such as P, and are thus expected to respond to N deposition differently than N-limited forests in the temperate zone. For example, some tropical forests grow on geomorphically stable, highly weathered soils that contain few remaining primary minerals, leading to low available pools of rock-derived nutrients such as potassium (K), calcium (Ca), magnesium (Mg), or P relative to N (Chadwick et al. 1999, Walker and Syers 1976). Other tropical forests, such as those in south Florida, are low in available P relative to N due in part to their growth on geologic substrates that lack P-bearing minerals or are subject to abiotic conditions that restrict P solubility (Noe et al. 2001, Troxler Gann et al. 2005). Additionally, many tropical forests support an abundance of legumes and other N-fixing plant species that can lead to large available N pools in soil (Vitousek et al. 2002), including both mature forests and successional plant communities that are recovering from agricultural abandonment (Erickson et al. 2001).

In these cases, plant growth can be limited by elements or factors other than N, which may limit the ability of these forests to retain atmospheric N deposition within plant reservoirs. Because N cycles in relative excess compared to other nutrients in these systems, these humid tropical forests exhibit naturally high rates of NO_3^- leaching and N trace gas emissions compared to temperate forests (Davidson et al. 2007, Lewis et al. 1999, Matson and Vitousek 1990, Martinelli et al. 1999; all in tropical forests worldwide). Thus, it has been hypothesized that N-rich, P-limited wet tropical forests are 'naturally N saturated' and will have little ability to retain additional N in biotic pools, possibly leading to elevated N losses to aquatic systems and the atmosphere (Hall and Matson 1999).

Few studies have tested this hypothesis at low levels of N inputs that simulate expected rates of atmospheric deposition in humid tropical forests of the United States and abroad. In a dose-response experiment in lower montane forests of Hawaii, Hall and Matson (1999) found immediate and elevated nitrous oxide (N_2O) and nitric oxide (NO) emissions from soils after first-time application of 15 kg N ha^{-1} as ammonium nitrate (NH_4NO_3) in a P-limited forest on the island of Kaua'i that received <1 kg N ha^{-1} yr^{-1} in ambient wet deposition (Carillo et al. 2002, Hall and Matson 1999). However, N-oxide emissions from this forest were not elevated following application of 5 kg N ha^{-1}. Similar patterns were found after a dose-response experiment in an N-rich, P-poor lowland tropical rain forest in southeast Asia that experienced higher rates of soil N-oxide emissions compared to unfertilized controls after application of 15 kg N ha^{-1} (Hall et al. 2004).

If excess N is not effectively retained in biotic reservoirs, N-rich tropical forests might also be expected to respond to N deposition with elevated NO_3^- losses. However, acidic, highly weathered soils often contain variably charged, subsurface, clayey horizons that can impede water infiltration and retain anions such as NO_3^- on clay particles. For example, in the same Hawaiian lower montane forests described earlier, Lohse and Matson (2005) found that NO_3^- leaching was restricted by clay layers in the P-limited forest after both first-time and long-term N fertilization with 50 kg N ha^{-1}, despite lack of retention by biota, whereas NO_3^- was readily leached after similar rates of fertilization in an N-limited forest that was well drained (Lohse and Matson 2005). Other factors associated with humid tropical forests may also favor NO_3^- retention, even when N cycles in relative excess. For example, forests in Puerto Rico support high rates of dissimilatory nitrate reduction to ammonia (NH_3) (DNRA), an anaerobic microbial process that consumes NO_3^- anions (Silver et al. 2001). DNRA was once thought to occur primarily in aquatic sediments but now appears to be a NO_3^- retention pathway favored by variable redox conditions characteristic of upland tropical forest soils (Pett-Ridge et al. 2006, Templer et al. 2008).

In N-rich humid tropical forests, it is expected that atmospheric N deposition will have relatively small direct effects on plant growth or community composition. For example, long-term N fertilization with 100 kg N ha^{-1} yr^{-1} had no effect on epiphytic cyanolichen abundance, diversity, or N-fixation capacity in P-limited and N+P co-limited lower montane rain forests in Hawaii (ambient N deposition < 1 kg N ha^{-1} yr^{-1} and ≤ 17 kg N ha^{-1} yr^{-1}, respectively) (Benner et al. 2007, Benner and Vitousek 2007, Carillo et al. 2002). Similarly, in an N-rich Hawaiian lower montane forest, N additions had no effect on plant growth or species richness and composition (Harrington et al. 2001, Ostertag and Verville 2002). Some responses to N deposition in upland tropical forests hold for mangrove ecosystems as well: fertilization with >100 kg N ha^{-1} yr^{-1} in a P-limited, dwarf black mangrove ecosystem in Belize had no impact on plant growth or morphology (Feller et al. 2007). Although N deposition may not alter plant growth in forests that are not limited by N, chronic N inputs to acidic, poorly buffered humid tropical forest soils may affect soil properties such as pH, aluminum mobility, and P fixation that may indirectly decrease tropical forest growth over the long term (Asner et al. 2001, Matson et al. 1999; both describing tropical forests worldwide). However, few studies have tested these hypotheses in the field.

While plant growth or community composition in relatively N-rich tropical and subtropical forests may not be affected by N deposition, tissue chemistry of

some plant species may be more sensitive to changes in N supply. For example, N additions increased foliar N concentrations and the decomposability of leaf and fine roots in P-limited Hawaiian lower montane forests (Ostertag and Hobbie 1999), and they increased litter N concentrations in lowland Panamanian forests that were not limited by N or P (Kaspari et al. 2008). However, based on the few studies that have measured these responses, this effect is not consistent across ecosystem types. For instance, N additions to a P-limited red mangrove stand in Belize and an N+P-limited red mangrove stand in Panama had no effect on foliar N or N:P ratios, or the amount of leaf area damaged by herbivores (Feller and Chamberlain 2007, Lovelock et al. 2004).

16.3.2 N-Poor Tropical and Subtropical Forests

While many humid tropical forests are relatively N rich, numerous processes can replenish rock-derived nutrients or increase N losses relative to other elements, thus promoting N limitation or conservative N cycling (LeBauer and Treseder 2008). These processes include deposition of transported dust or sea salt aerosols, erosion, fire, and other disturbances such as forest clearing that increase N losses or N sinks in vegetation (Chadwick et al. 1999, Davidson et al. 2007, Porder et al. 2005, Scatena and Lugo 1995; in Amazon forests). For example, much of the forested land area in Puerto Rico is successional, as >75 percent of the landscape is affected by hurricanes or landslides each century (Lugo and Scatena 1996, Walker et al. 1996). These disturbances can cause N losses to the atmosphere and water that may remain elevated for years until biological sinks are re-established (Erickson and Ayala 2004, McDowell et al. 1996, Schaefer et al. 2000). Combined, these spatially and temporally heterogeneous factors will likely cause variation in the extent of N retention in humid tropical and subtropical forests in response to atmospheric N deposition.

Measures of nutrient availability are often correlated with the responsiveness of plant growth to fertilization but are not sufficient to establish nutrient limitation (Tanner et al. 1998). However, evidence in the literature suggests that many tropical forests in the United States with low N availability will respond to N deposition in ways similar to temperate forests, with increased rates of primary production and foliar N concentrations, and potentially increased soil N cycling and N gas emissions over time. For example, emissions of N_2O and NO were elevated after 6 years of complete nutrient additions (300 kg N ha^{-1} yr^{-1} and 100 kg P ha^{-1} yr^{-1} plus cations; ambient deposition of 4 to 9 kg N ha^{-1} yr^{-1}) in a >60-yr-old tropical forest in Puerto Rico that cycled N conservatively (Erickson et al. 2001, Ortiz-Zayas et al. 2006). In a strongly N-limited, lower montane forest on the island of Hawai'i, NO_x emissions were elevated, but relatively low after application of ≥25 to 50 kg N ha^{-1}, but long-term N additions of 100 kg N ha^{-1} yr^{-1} increased rates of net N mineralization and nitrification in soils (ambient deposition of 17 kg N ha^{-1} yr^{-1}, primarily as fog from active volcanic sources) (Carillo et al. 2002, Hall and Matson 2003). Long-term N additions to this N-limited Hawaiian lower montane forest also altered species composition and decreased species richness, moss cover, and native seedling abundance (Ostertag and Verville 2002). However, decomposition rates were not affected by N additions, suggesting that carbon (C) mineralization rates were limited more strongly by C quality than nutrient availability (Hobbie 2000).

Growth of mangrove forests in Florida is limited by N in some regions and P in others, varying across small scales within mangrove stands (Feller et al. 2003b, 2007) and across landscape gradients of tidal inundation that restrict availability of nutrients under saline conditions (Boyer 2006, McKee 1995). In an N-limited black mangrove ecosystem in Florida (ambient deposition ~ 4.1 kg N ha^{-1} yr^{-1}) (Caccia and Boyer 2007), N additions of >100 kg N ha^{-1} yr^{-1} increased growth (wood allocation and shoot elongation), altered foliar chemistry (increased N and P resorption efficiency and foliar N concentrations; decreased C:N ratios of green and senescent tissue), and increased herbivory by some species (Feller et al. 2007). Plants are known to decrease N resorption from senescing tissue with increasing N availability, although the strength of this process varies widely across species (Norris and Reich 2009). In N-limited lagoons in Florida, increased N

resorption in N fertilized mangrove stands may have resulted from simultaneous changes in P dynamics (Feller et al. 2007). In contrast, N fertilization had no effect on leaf area ratio, specific leaf area, photosynthetic rates, or hydraulic traits of N-limited black mangrove stands (Lovelock et al. 2006). Other work shows that the impact of N enrichment may also depend on species composition. For example, Feller et al. (2003b) and Lovelock et al. (2004) found that N fertilization had no impact on N resorption efficiencies in N+P-limited red mangroves in Panama or N-limited (seaward fringe), N+P-limited (transition zone), or P-limited (forest interior) red mangroves in Belize. Also, unlike in N-limited black mangroves, N fertilization in N+P limited red mangroves in Panama had no effect on the fraction of leaf area damaged by herbivores (Lovelock et al. 2004).

Although N may be retained in some N-poor tropical forests as in temperate systems, the mechanisms of N retention may differ depending on the structure of tropical plant communities. For example, high year-round leaf area of tropical forests may act to retain N in canopies, intercepting N deposition before it reaches microbial and plant communities of the soil and forest floor (Bakwin et al. 1990, Sparks et al. 2001). In a study of cloud forests in Costa Rica, epiphytes within the canopy retained 50 percent of the N applied experimentally in the laboratory and field, leading to higher foliar N concentrations in bryophyte species (Clark et al. 2005). In mangrove ecosystems of Belize, ammonium (NH_4^+) in bulk precipitation was retained in the canopy in an N-limited stand, but not in a P-limited stand, decreasing throughfall fluxes of N compared to rainwater (Wanek et al. 2007). These data suggest that change in composition or chemistry of foliage or canopy epiphyte communities may indicate initial stages of N saturation of tropical forest ecosystems.

Finally, recent work suggests that after disturbance in some tropical forests, N limitation may be short-lived. For example, tropical forests in the Amazon supported low rates of N cycling early in succession following agricultural abandonment, but returned to 'leaky' N cycling similar to N-rich, mature tropical forests within decades (Davidson et al. 2007).

16.4 Critical Loads Estimates

Estimates of critical loads of N in the U.S. Tropical and Subtropical Humid Forests ecoregion are uncertain due to lack of data across N deposition gradients or from low-level N addition studies. Furthermore, critical loads will depend on the form of N inputs and numerous ecosystem characteristics that influence N retention, most of which vary considerably across tropical and subtropical forests. These factors include, among others, the form of N deposition (NH_4^+ vs. NO_3^-), the extent of N limitation of primary production; spatial and temporal heterogeneity in soil organic matter, water-holding capacity, and moisture that can influence microbial N cycling processes (e.g., nitrification and dentrification); subsurface soil properties that may alter N leaching (e.g., retention or loss of NH_4^+ or NO_3^- from deposition will depend on soil texture and cation vs. anion exchange capacity); and composition of heterogeneous and diverse plant communities. However, in the absence of data, we estimate critical loads of 5 to 10 kg N ha^{-1} yr^{-1} for N-poor tropical and subtropical forests (e.g., some mangrove ecosystems in Florida, early successional forests or forests growing on pedogenically young substrates), within the same range as forests in the Southeastern Coastal Plain that may have similarly weathered soil types and experience warm year-round temperatures. Critical loads for N-rich tropical and subtropical forests may be lower than this level if N deposition rapidly stimulates pathways for N loss. Thus, we estimate critical loads of <5 to 10 kg N ha^{-1} yr^{-1} for N-rich tropical and subtropical forests.

16.5 Comparison to Critical Loads for Other Regions

Few estimates exist for N critical loads in tropical and subtropical forests. Studies in south China recommend high critical loads of 50 to >150 kg N ha^{-1} yr^{-1} to prevent departure from current conditions based on fertilization experiments across a range of ecosystem types (reviewed in Duan 2009). However, N deposition to Chinese subtropical forests ranges from at least 8 to 50 kg N ha^{-1} yr^{-1} (Chen and Mulder 2007a, Chen and Mulder 2007b). Thus, it is impossible to determine whether current conditions represent a change from conditions prior to elevated N deposition. Furthermore,

species composition within Chinese subtropical forests varies considerably from tropical and subtropical forests in the United States. As a result, it is unclear whether critical load estimates developed for China are applicable to forests reviewed in this chapter.

16.6 Future Research, Gaps in Data, Gaps in Knowledge

Currently, tropical and subtropical forests in the United States are highly fragmented and are threatened primarily by land-use change, invasive species, and nutrient pollution from agricultural runoff. Consequently, to date no studies have evaluated the ecological consequences of atmospheric N deposition in these regions. Refined estimates of N critical loads for this ecoregion will require studies that explore ecological processes across N deposition gradients or following low-level N additions.

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