

15. Summary of Prospective Global Change Impacts on Northern U.S. Forest Ecosystems

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In January 1989, the President's Fiscal Year 1990 Budget to the Congress was accompanied by a report entitled, "Our Changing Planet: A U.S. Strategy for Global Change Research" (Committee on Earth Sciences, 1989). The report focused the attention of policy makers on the significant environmental issues arising from natural and human-induced changes in the global Earth system. The report announced the beginning of a research program, the U.S. Global Change Research Program, with a mission to improve our understanding of the causes, processes, and consequences of the changes affecting our planet. Interest in global change was heightened in 1990 with the publication of "Climate change: The IPCC Scientific Assessment" (Houghton et al., 1990) by the Intergovernmental Panel on Climate Change (IPCC), jointly sponsored by the World Meteorological Organization and the United Nations Environmental Program. This assessment was updated and new technical issues were added in the second assessment volumes, "Climate Change 1995: The Science of Climate Change" (Houghton et al., 1996) and "Climate Change 1995: Impacts, Adaptations, and Mitigation of Climate Change" (Watson et al., 1996). The first IPCC assessment in 1990 and subsequent assessments have concluded that continued accumulation of anthropogenic greenhouse gases in the atmosphere will lead to climate change whose rate and magnitude are likely to have important impacts on natural and human systems. Concurrent with these reports, several scientific literature reviews and research summaries by Eamus and Jarvis (1989), Bazzaz (1990), Musselman and Fox (1991), Strain and Thomas (1992), Rogers and Runion (1994), Gunderson and Wullschleger (1994), Ceulemans and Mousseau (1994), Idso and Idso (1994), Curtis (1996), and Mickler and Fox (1998) have quantified the direct effects of rising carbon dioxide (CO₂) on plant growth and development. Unlike the statements made with scientific certainty in the 1970's which heralded the beginning of the *Waldsterben* or "forest decline" in Germany, Europe, and the U.S. but concluded with the uncertainty associated with characterizing the effects of multiple stressors on forest ecosystems, predictions of global change and its effects began in the 1980s by acknowledging many uncertainties. Today, scientific assessments of climate change are characterized by ever increasing scientific understanding and improved predictive capabilities.

This volume summarizes the progress in our understanding of how multiple interacting stresses associated with global change are affecting or are likely to affect northern U.S. forest ecosystems at multiple spatial and temporal scales. In this summary chapter we attempt to draw conclusions from the material presented, and highlight a few dominant themes from these studies and others that comprise several decades of environmental effects research. We are only beginning to understand the paleoecology of northern forest ecosystems and how these forests are likely to evolve over the next century. Our goal has been to assemble the available though incomplete knowledge of current and prospective responses of northern forest ecosystems to multiple environmental changes, to develop a scientific basis for planning future global change research, and to transfer available information to land managers and policy makers.

Characteristics of Northern Forests and Their Environment

Current Forest Conditions and Trends in Carbon Sequestration

The northern region contains 23% of the forest area of the U.S., 18% of the land area, and 45% of the population. The region is unique in that heavily forested areas are located near areas of high

population density. As a result, forest fragmentation has become a major issue for the region. Private forest landowners control 80% of forest land. Most of the private owners own timberland primarily for recreation and esthetic enjoyment. However, one third of private owners managing 61% of private forest lands intend to harvest their forests in the next 10 years.

Northern U.S. forests had been cleared for agriculture or heavily logged by the mid-1800s. Harvesting of forests in the Lake States removed the climax pine-hemlock (*Pinus* spp.-*Tsuga canadensis* [L.] Carr), and agricultural land clearing and fire is responsible for the present northern conifer, hardwood, and mixed forest of New England states. Since the 1920s, reestablishment and regrowth of forests on farmed or logged land has resulted in the large areas of maturing forest common today. The region is still gaining forest land from other uses, primarily agriculture. The most recent inventories by the USDA Forest Service Forest Inventory and Analysis Program indicate a 4% increase, despite continued development and fragmentation in some areas.

A major event shaping the species composition of today's forest was the chestnut blight, which all but eliminated this important species by mid 20th century. Oaks (*Quercus* spp.) and other hardwoods replaced this once-dominant species. Oak-hickory (*Carya* spp.) and maple (*Acer* spp.)-beech (*Fagus* spp.)-birch (*Betula* spp.) forest types together account for over 60% of the forest area, with oak-hickory common in the southern part of the region and maple-beech-birch common in the northern part of the region. The aspen (*Populus* spp.)-birch type is common in the North, particularly in the Lake States. The most northern parts of Maine and the Lake States contain significant amounts of spruce (*Picea* spp.)-fir (*Abies* spp.). In terms of timber volume, the North contains 47% of the nation's hardwood volume but only 11% of the nation's softwood volume. Lack of oak regeneration following harvest is a major issue for the region, as loss of oak forests coupled with a major expansion of red maple results in lower economic value and reduction of important mast species. Areas of major pest problems include spruce-fir forests in Maine, heavily damaged by spruce budworm in the 1980s, and the Allegheny Plateau region of Pennsylvania, where numerous biotic and abiotic agents have caused damage and decline of sugar maple.

Northern forests contain large reservoirs of carbon (C) in maturing forests and forest soils. Northern forests are estimated to contain more carbon than forests of the southern and western regions of the U.S., and are projected to continue to contain more carbon (Birdsey and Heath, 1995). In 1992, northern forest ecosystems contained an estimated 13.4 Pg C, with a rate of increase of 0.16 Pg C yr⁻¹. Projections through 2040 indicate that northern forest ecosystems will contain 17.5 Pg C with a rate of increase of 0.08 Pg C yr⁻¹. Comparable estimates for the Southern U.S. are current storage of 11.5 Pg C increasing at 0.03 Pg C yr⁻¹, and projections through 2040 indicating future storage of 11.9 Pg C and an average rate of increase of 0.03 Pg C yr⁻¹. Comparable estimates for the Western U.S. are current storage of 12.9 Pg C with a rate of increase of 0.02 Pg C yr⁻¹, with projections through 2040 indicating future storage of 16.8 Pg C and an average rate of increase of 0.08 Pg C yr⁻¹. Although northern forests generally do not grow as fast as southern forests, they are not harvested as heavily which leads to the increases in carbon inventory. In the recent past, forest growth has been more than twice forest removals. Expected increases in harvesting coupled with slower growth characteristic of aging forests will reduce the high rate of carbon sequestration over the next 50 years or so.

Northern Forest Soils and Nutrient Depletion

Soil may be the most important factor that determines health and productivity of forests. Nutrient depletion as a consequence of decades of acid deposition and intensive land use are of particular interest in the North, and the subject of much research over the last two decades. To

compile complete nutrient budgets for forest ecosystems, researchers have begun to study the influence of bedrock on nutrient and water cycling, which may be minimal where thick surficial deposits cover the bedrock, and great where surficial deposits are shallow.

Soil taxonomic units provide a convenient framework to examine effects of environmental change on soil and forest resources. Taxonomic units reflect differences in age of parent material, texture, and composition, which interact with climate, topography, and vegetation to determine water and nutrients movement through the soil profile, deposition affects on water and nutrients, and differing nutrient content and flux rates.

Depletion of base cations is a critical issue for northern forest soils and is recognized as an important long-term problem in southern U.S. soils (Richter and Markewitz, 1996). If weathering of parent material is not sufficient to replace base cations lost to forest growth and leaching, then depletion is likely. Mass balance studies show that depletion of base cations is a problem at some specific sites, but spatial variability of forest soils has hindered accurate extrapolation of these observations to landscape and regional scales. Improved models of susceptibility to nutrient depletion will likely follow better understanding of spatial patterns of the mineralogic composition of soil parent materials, and better knowledge of the mechanisms and locations of weathering patterns at the landscape scale.

Climate and Atmospheric Deposition Changes

Atmospheric CO₂ concentration has increased by 25% in the last century and is expected to increase globally 1.43 $\mu\text{L L}^{-1}$ each year, to a doubling or more of historical concentrations during the middle of the next century. Coupled with increases in other greenhouse gases (e.g., methane, nitrous oxide, and halocarbons), these atmospheric changes are expected to cause significant warming of the earth's surface. How such climate change would affect the northern region depends in large part on changes in the development and behavior of weather systems affecting the region. However, projecting these changes is highly uncertain because of the extreme complexity of earth-atmosphere interactions, and an inability to account for small-scale weather phenomena in global circulation models.

Global-scale model simulations of future climate conditions suggest a global average temperature increase of between 1.0° and 4.5°C with a doubling of atmospheric CO₂ (Houghton et al., 1996). The greatest warming is expected over land and at higher latitudes. On a seasonal basis, warming is expected to be most significant in late autumn and winter. All models project an increase in global precipitation, particularly in the winter over northern and mid-latitudes. Global models currently do not have the capability to make predictions of changes in extreme weather events, although such changes are theoretically possible.

Over North America, the most significant observed temperature changes over the last 40 years have occurred from the North Central U.S. through Northwestern Canada into Alaska. Average surface temperatures have increased from 0.25° to 1.5°C over this region. On a seasonal basis, the most significant changes occurred during the winter and spring. Some areas within the Northern Region, particularly in the west and north, have experienced a large number of extreme maximum and minimum temperature events over the last 40 years. Other notable temperature events include late spring freezes and midwinter thaws. Thaws followed by rapid freezing can be particularly damaging to vegetation.

Precipitation patterns are highly variable and more unpredictable than temperature changes. Precipitation in the Northern Region has increased an average 2 to 5% per decade since 1900.

Extreme precipitation events and droughts occur periodically in different parts of the region. Such extreme events are manifestations of atmospheric circulation patterns that can be associated with probabilities of event occurrence. A well-known example of such a circulation pattern is the El Niño/Southern Oscillation, driven by changes in Pacific Ocean surface temperatures. El Niño events have the largest effect on the U.S. during the winter and early spring months. In the Northern region, the risk of extreme precipitation in the winter months is particularly high in the central and southern Great Plains, based on observed precipitation patterns.

Atmospheric deposition patterns are determined by air pollution concentration gradients associated with emission sources, meteorological conditions, topography, and prevailing air transport patterns. The Northeast and North Central regions of the U.S. contain a high concentration of pollution sources, but the pattern of pollution exposure varies markedly within the region from the highest national exposure levels to unpolluted background levels.

Acid deposition patterns reflect the emissions source areas in the Ohio River Valley and the Midwest, and the prevailing winds which deposit the highest acidity to a region including eastern Ohio, northern West Virginia, western Pennsylvania, and western New York. Other areas of high acid deposition include the Adirondack Mountains and Catskill Mountains of New York. Nitrogen (N) deposition, of particular interest because of its effects on forest processes, ranges from approximately 2.5 kg ha⁻¹ in northern Maine to more than 20 kg ha⁻¹ in Pennsylvania.

Recent changes in deposition have resulted from the passage of the 1990 Clean Air Act (Stoddard et al., 1999). During the period between 1983 and 1994, deposition of sulfur (S) compounds and hydrogen ions has decreased significantly, 10 to 25% and 12%, respectively. Nitrogen deposition increased nationally for the same period.

Ozone (O₃) concentrations over urban/industrial areas of the northern U.S. average about twice background levels, or 80 ppb. The highest exposures occur in the Washington—New York corridor, and lowest levels in northern Minnesota and northern Maine. Ozone concentrations vary greatly across time and space. There is a tendency for areas of high O₃ exposure to also have high deposition of N and S compounds.

Incidence and Causes of Forest Declines

Decline diseases, linked to stress and environmental change, have increased over the past century and in particular in the last two decades. A well-developed theoretical basis explains decline diseases in terms of the interactions between predisposing factors, inciting factors, and contributing factors. If the theoretical models are correct, then increased levels of various interacting stressors in the Northeast are likely to lead to increased incidence of decline disease. Decline diseases are commonly associated with leaf anomalies (e.g., reduced leaf size, scorch, necrosis, premature coloration, and leafdrop), progressive crown dieback, reduction in radial and terminal stem growth, and reductions in root carbon reserves. Increasing environmental stress is occurring at the same time as many species reach biological maturity across much of their range, a consequence of past land use impacts. Aging forests are known to be more susceptible to decline disease.

Drought and defoliation are the most common stressors associated with decline disease in the Northeast. Other important stressors include sucking insects defoliation from late spring frost, and fungal leaf pathogens. Examples of the occurrence of decline disease include: (1) sugar maple (*Acer saccharum* Marsh) decline in northwest Pennsylvania associated with biotic factors (defoliating insects, borers, and canker fungus), a series of droughts, and acid deposition; (2) red spruce (*Picea rubens* Sarg.) decline in the Northeast associated with winter injury induced by acidic deposition; and

(3) a series of widespread and simultaneous declines associated with climatic extremes over the last century. The extent and severity of declines seems to be higher over the last 25 years compared with the previous 75 years.

Physiological Responses of Trees to Environmental Change

Interacting Effects of Multiple Stresses

Two pollutants that have substantial impacts on plant growth and are increasing in the atmosphere as a consequence of human activity are CO₂ and O₃. Plant responses to CO₂ and O₃ are complex, and become even more difficult to interpret when other known stressors are considered, including N limitation, temperature and moisture extremes, and pests. In general, increasing atmospheric CO₂ increases photosynthetic rates, height growth, and biomass production, while increasing atmospheric O₃ decreases photosynthetic rates and biomass production, and increases leaf senescence. The amount and sometimes the direction of change depends on internal plant factors, such as age and genotype. Higher CO₂ concentrations may compensate for some other environmental stresses (see review by Mickler, 1998). For example, most studies show that CO₂ enrichment increases growth even though light and/or nutrients are limiting. It is becoming clear that both increasing CO₂ and O₃ impact fundamental plant processes, which in turn affect susceptibility to plant-feeding insects.

Studies on trembling aspen (*Populus tremuloides* Michx.) show that O₃ usually decreases growth although the effect varies significantly with genotype. Similar results have been reported by Flagler et al. (1998) in shortleaf pine (*Pinus echinata* Mill.) and in other southern pine species (see research program findings by Fox and Mickler, 1996). Root growth appears particularly sensitive to O₃. In contrast, substantial increases in relative below-ground C allocation were found in response to elevated CO₂. Experiments with both elevated CO₂ and O₃ suggest that elevated CO₂ does not compensate for reduced growth caused by elevated O₃. When N limits growth, there appears to be no response to elevated CO₂. Because CO₂ and O₃ change the chemical composition of the foliage, resistance to insect attack and nutritional value of foliage are altered. Elevated O₃ appears to increase insect growth and elevated CO₂ decreases insect growth. Under field conditions, these changes in insect physiology may offset increases or decreases in biomass production with elevated CO₂ that are associated with a changing atmosphere.

Consistent growth responses of yellow poplar (*Liriodendron tulipifera* L.) to O₃ have not been reported even though the species shows visual foliar symptoms of exposure. One study reported an increase in biomass production during the first year of exposure in open-top chambers, and a decrease after two seasons. Elevated CO₂ appears to increase yellow poplar growth regardless of level of exposure to O₃. In general, research on yellow poplar suggests that under field conditions, this species will increase biomass production even when nutrients and moisture are limited and in the presence of O₃.

Experimental methods have a major impact on how results from these studies should be interpreted. Significant chamber effects are common, limiting extrapolation of many experimental results to field conditions. Because experiments are typically short-lived and employ a large step increase in simulated exposure (as opposed to a gradual increase), there is no direct evidence showing how changing atmospheric chemistry would affect plant processes over the long term. Extrapolations of experimental results to natural ecosystems using process models have concluded that the long-term effects of increasing atmospheric CO₂ are likely to decline in magnitude over time (Luo, 1999). However, field exposures of loblolly pine seedlings (Alemayehu et al., 1998), saplings (Dougherty et

al., 1998; Hennessey and Harinath, 1998), and mature trees (Teskey, 1998) to elevated CO₂ have not demonstrated any acclimation. Open-air exposure experiments and field physiological studies conducted over long time periods will eventually increase our understanding of individual species and forest community responses to elevated CO₂ and global change stressors as will improvements of physiological process models.

Winter Injury to Red Spruce

There has been an increase in the incidence of freezing injury to northern mountain red spruce forests and red spruce forests at lower elevations, leading to forest decline, over the past five decades (Eagar and Adams, 1992). Red spruce winter injury has been caused by subfreezing temperatures, and the species has only sufficient midwinter cold tolerance to protect foliage from the minimal temperatures found in its northern mountain range. It is likely that the increased injury is the result of acid deposition and climate perturbations. Red spruce is much more susceptible to freezing injury than the co-occurring species balsam fir (*Abies balsamea* [L.] Miller).

Many environmental factors have been studied for their potential to reduce cold tolerance. Ozone does not appear to reduce foliar cold tolerance or increase susceptibility to freezing injury. Carbon dioxide enrichment and N nutrition may interact to influence cold tolerance but the evidence is not clear. It is virtually certain that rapid freezing stress explains localized injury concentrated on sun-exposed branches, but it is unlikely that rapid freezing explains injury on shaded foliage or regionwide injury events. Long winter thaws (4 to 5 days) cause reductions in cold tolerance of up to 14°C, a response unique to red spruce. Numerous studies have shown that short-term N additions either have no impact on freezing tolerance or may improve hardiness. Sulfur additions appear to have some impact on autumn hardiness, but no impact on winter cold tolerance. Aluminum (Al) has many effects on red spruce physiology, but no apparent effect on cold tolerance. Calcium (Ca) loss due to acid deposition affects red spruce health, and may have indirect effects on cold tolerance. The strongest evidence for an environmental effect on freezing injury is that exposure to acid cloud water increases the risk of foliar freezing injury by reducing the cold tolerance of current-year foliage from 5° to 12°C. Of all the possible combinations of factors, interactions between acid mist and thaw have the greatest potential to increase the risk of freezing injury during winter, but this hypothesis has not been fully tested.

The specific mechanisms causing winter injury appear to include perturbations of winter temperatures on a species with limited genetic potential for cold tolerance, coupled with alterations to the structure and function of plasma membrane-associated Ca in mesophyll cells (DeHayes et al., 1999). Acid-leached calcium is primarily derived from current-year needles and increases hydrogen ion uptake 60 times in response to acidic mist. Acid mist-induced calcium losses in needles reduces membrane stability and decreases freezing tolerance 4° to 10°C. Because of the strong linkage of this mechanism to acidic precipitation, there is great concern that membrane integrity of other species may also be affected, but only red spruce exhibits visible damage symptoms because, of its susceptibility to winter injury.

Acid Deposition and Tree Health

Tree rings are good measures of growth and indicators of health. Tree ring characteristics are a composite response to intrinsic and extrinsic factors, and although growth is integrative, it is restricted by the essential factor that is most limiting in supply. Trees sampled at or near the edge of their range

are likely to contain a stronger common signal, especially of climate. Given these principles, the use of tree rings as a proxy record of climate or environmental disturbance depends on uniformity of linkage between external conditions and tree biology. Separating the signal of external and internal factors in the tree-ring record can be difficult.

Based on a large sample of red spruce tree rings, enrichment of Ca and magnesium (Mg) evident in stemwood formed in the 1960s is consistent with the mobilization of base cations in the soil, which also coincides with increases in the atmospheric deposition of nitrates and sulfates. Root physiology and pathology are affected indirectly by acidic deposition, through changes in soil chemistry and C allocation patterns to the roots. The Ca/Al molar ratio of the soil solution seems to be one of the prime mechanisms by which acidic deposition affects forest growth and is an important indicator of potential stress.

The availability of biological markers that can assess the current status of stress in apparently healthy trees in a forest is crucial for planning a potential treatment or management practice for mediating or removing the stress. In conjunction with soil chemistry, putrescine and/or spermidine may potentially be used as early indicators of Al stress before the appearance of visual symptoms in red spruce trees. The combination of Al induced growth suppression in soils with air pollutant induced growth suppression may be a major cause of tree mortality.

Ecosystem Responses to Environmental Factors

Atmospheric Deposition Effects

Research during the 1980s yielded conclusive evidence that acidic deposition had acidified poorly buffered surface waters causing loss of fish populations and other aquatic organisms. Although acidic deposition affected soil chemistry, effects on forest health were not apparent, with the exception of stand dieback of high elevation red spruce. The National Acid Precipitation Assessment Program (NAPAP) provided much information about natural processes within aquatic and forest ecosystems, and initiated baseline monitoring of deposition rates and chemical changes in ecosystems. NAPAP also highlighted the importance of interactions between multiple stressors, which together threatened the long-term structure, function, and productivity of ecosystems by changing chemical composition and nutrient cycling. In particular, it was noted that acidic deposition could decrease nutrient retention in forest ecosystems and cause imbalances in the availability of nutrients (NAPAP, 1991).

Research in the 1990s began to address the issue of recovery following declining acid deposition rates. Researchers demonstrated the complex interactions between precipitation, soil characteristics, and downstream processes. For example, release of nitrate from watersheds is controlled by biological processes that determine N mobility within soils, not hydrologic transport of atmospherically deposited N directly through soils into surface waters. Also, the importance of the forest floor in supplying Ca for root uptake was noted, along with the regional decline of available Ca that had occurred in the second half of the 20th century. Important mechanisms causing Al mobilization were discovered. Acidic deposition lowers the pH of the mineral soil, causing mobilization of Al that can then be transported into the forest floor, reducing the amount of available, Ca. There seems to be a strong connection between soil Ca availability and the health and long-term growth rates of sugar maple; however, this is part of a complex of factors rather than a single factor effect (Horsley and Long, 1999).

Deposition of N may cause ecosystem saturation and a possible shift in species composition because of differential utilization by deciduous and coniferous species. Growth responses to N

additions depend not only on species but on tree health and availability of nutrients in the soil, in particular, the availability of Ca. Nitrogen additions cause decreases in C allocation to fine roots, with implications for uptake of other nutrients. However, N may also increase the retention of nutrients on the site through a series of processes involving litter quantity and quality, microbial activity, and water retention capacity.

Poor air quality in urban areas may affect plant biota and biogeochemical processes. Based on a study of oak stands along an urban-rural gradient, there is evidence that deposition of heavy metals affects litter fungi, but inconclusive evidence that acid deposition affects soil properties (Pouyat et al., 1995a). Ozone damage has been suggested as a possible cause of changes in litter quality along the urban-rural gradient (Pouyat et al., 1995b).

Nitrogen Saturation

In the U.S. the concept of nitrogen saturation is variously defined as (1) the absence of a growth response in vegetation to N additions, (2) the initiation of nitrate leaching, or (3) the lack of net N accumulation in ecosystems as evidenced by an equivalence between inputs and losses. The region of the U.S. that is most susceptible to N saturation, due to high inputs of N, is the Northeast and in particular high elevation sites where deposition is the greatest. Many factors affect the susceptibility of a forest site to N saturation, including vegetation type, soil characteristics, and land use history.

Watershed-scale additions of N at both Bear Brook in Maine and the Fernow Experimental Forest in West Virginia have clearly shown that the majority of deposited N is retained even in ecosystems showing symptoms of N saturation, although increased stream export of NO_3 was evident. Somewhat scanty evidence suggests that some of the N is retained in vegetation, and that more is likely retained in the soil. However, the mechanisms responsible for N retention are unknown, as are the consequences for forest management and the potential for recovery if N inputs are reduced. There is no conclusive evidence that increased N inputs have resulted in increased vegetative growth and some evidence indicates that the forest growth is still N limited.

Response of Forest Soils to Warming

Experimental evidence supports the hypothesis that an increase in soil temperature of 1.0° to 3.5°C can have significant effects on belowground C and N cycling in northern U.S. forests. Soil C and N cycling are important because of the potential feedbacks to the atmosphere which could affect the direction and magnitude of climate change, the relationship of these cycles to forest productivity and health, and the potential for nutrient export from watersheds to sensitive downstream wetlands and coastal water bodies.

The responses of soils processes to experimental warming are mixed. Soil respiration and N mineralization showed significant and consistent increases regardless of site or treatment. Oxidation of methane, nitrous oxide flux, and litter decomposition showed variable responses that depended on litter quality, N availability, and soil moisture.

Observations along a latitudinal gradient in Michigan suggest that warmer soil temperatures contribute to greater fine root mortality (Hendrick and Pregitzer, 1993). Faster root turnover is one controlling factor for below-ground carbon and nutrient cycling.

Because of the complexity of belowground processes and lack of knowledge with which to construct definitive process models, it is not possible to state whether northern U.S. forest soils will be a net source or sink of C as a consequence of atmospheric warming. However, the balance of

experimental evidence and observations suggests that increased soil respiration and litter decomposition, together with decreasing soil organic matter from increasing temperature, will result in a net efflux of C from the soil to the atmosphere. Other possible responses that could counteract this effect include increased N availability and, therefore, increased net primary productivity (NPP) in N limited ecosystems, which could increase the rate of C uptake by plants. However, in N-saturated systems, which are rarer (but increasing from N deposition) than N limited systems, C uptake could decrease as a consequence of deteriorating forest health.

If temperature changes are small, regional effects on ecosystems are likely to be insignificant relative to more pronounced effects from harvesting, insects and diseases, and other disturbances. Nonetheless, because of the ubiquitous nature of prospective warming, even a small effect spread over a large area could be significant.

Regional Impacts of Multiple Stresses on Productivity and Health

Effects of Increased Carbon Dioxide and Climate Change on Productivity

Changes in NPP of forest ecosystems in the Northeast in response to increasing atmospheric CO₂ and scenarios of climate change were estimated with two ecosystem process models, PnET-II and TEM 4.0. Models were used for this regional analysis because of complex interactions at the ecosystem scale between CO₂ response, biogeochemical cycles, and water and energy fluxes. The two models differ in their representation of above- and belowground processes, their mechanisms of response to CO₂, and their approaches to regional parameterization. To the extent possible, input data was consistent for the two models in order to illustrate similarities and differences in NPP predictions for the region in response to enhanced CO₂ and climate change.

At the regional scale, both models predicted an increase in productivity under climate change scenarios, with PnET-II predicting an average increase of 37.9% and TEM 4.0 an average increase 30.0% for contemporary climate. There was a large difference in model predictions for different climate change scenarios, with the models differing by 3% for contemporary climate and by 10% for the future climate scenarios. PnET-II predicts higher productivity in hardwood and hardwood-pine forest types whereas TEM 4.0 predicts approximately the same productivity for forest biomes. Estimates of NPP with PnET-II showed more sensitivity to different forest types. The NPP responses in TEM 4.0 appear to be limited by temperature, while PnET-II appears to be limited by water. Differences in model structures and representations of response to increased CO₂ contributed to variability in predictions of future productivity. Neither model included some factors known or suspected to influence productivity, such as transient (as opposed to step-wise) climate change, N deposition, and past land use.

The responses of NPP to doubled CO₂ alone were investigated with three biogeochemistry models in the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP). For the conterminous United States, doubled atmospheric CO₂ causes NPP to increase from 5-11% according to these model results (Pan et al., 1998). The national C accounting model (FORCARB) indicates that with an average increase in productivity as predicted with the TEM model, forest trees in the northeast and north central U.S. will have sequestered 19% more C as compared with a business-as-usual scenario (Birdsey and Heath, 1995).

Based on these modeling studies, and considering the experimental evidence, it is likely that the combined effects of increased atmospheric CO₂ and projected climate change will increase forest productivity. Uncertainty in this conclusion is related to the high uncertainty in the projected effects of

increasing greenhouse gases on precipitation. An increase in temperature accompanied by a decrease in precipitation could cause plant stress and a reduction in NPP. The magnitude of the water stress would be ameliorated to some degree by CO₂-induced stomatal closure, which increases water use efficiency, a result found in many experimental studies (Tyree and Alexander, 1993).

Ozone Effects on Productivity

Mechanistic models simulate changes in forest structure or function by quantifying fundamental mechanisms or processes, whereas statistical models rely on analysis of empirical data. Mechanistic models can therefore be used to extrapolate forest responses beyond conditions that have already occurred, if the appropriate response mechanisms are understood and modeled correctly.

PnET-II, an ecosystem-scale model used to estimate regional forest production of hardwoods, total ecosystem C balances and water yield, and responses to climate change, was modified to include O₃ effects on productivity including interactions with other stressors. Predicted NPP ranged from 750 to 1450 g m² yr⁻¹ and generally increased from north to south across the region. The model was then modified to include leaf-level uptake-response relationships and allow interaction with factors such as light attenuation, canopy ozone gradients, and water stress. Results for New England and New York showed decreases in predicted annual NPP from 2 to 17% as a result of mean O₃ levels from 1987 to 1992, with greatest reductions occurring where both O₃ levels and stomatal conductance were greatest. Growth declines were greatest on sites with wetter soils.

Another approach to estimating O₃ effects was to couple a model of forest stand development and composition (ZELIG) with a model of tree-level physiological response to stress (TREGRO). TREGRO models the acquisition of C, water, and nutrients, and allocates C among competing plants parts depending upon resource availability and phenology. ZELIG is a gap-succession model used to simulate succession in mixed stands typical of eastern and northern forests, and has both mechanistic and empirical characteristics. The two models were coupled by passing calculations from TREGRO to ZELIG in order to modify the growth relationships in the stand model. Simulated response to ambient O₃ from 1991 using the TREGRO/ZELIG combination for red oak and sugar maple in the Northeast showed a 2 to 4% reduction in red oak basal area growth over a 100-year simulation and a 3 to 12% growth increase in sugar maple across the region due to reduced competition from ozone sensitive species.

Model predictions include uncertainty due to (1) incomplete regional data, (2) incomplete knowledge of how forests respond to particular stresses, and (3) uncertainty about which processes and parameters should be included in the model. Some of this uncertainty is related to spatial interpolation, aggregation, and scaling errors.

Effects of Climate Change on Forest Insect and Disease Outbreaks

There is much uncertainty in predictions of the effects of climate change on insects and diseases. Effects can act directly on the physiology of the organisms, and indirectly through interactions with physiological changes in host plants or natural enemies.

Considering only the direct effects of warming, most insect species would survive more successfully over winter. Also, many insect species would shift their ranges toward higher latitudes and elevations, but this response is partly dependent on concomitant host and enemy changes. Species with flexible life histories could produce more generations per unit of time, as has already happened

with the spruce bark beetle in Alaska. In summary, direct effects of warming are likely to increase the frequency, level, and geographical extent of disturbance by insect pests.

Indirect effects are more subtle and, therefore, more difficult to predict. Population changes of defoliators, such as gypsy moth and spruce budworm, are governed by complex interactions with hosts and natural enemies. For example, the effects of increased CO₂ on insects is mediated by changes in foliar nutrition and presence of defensive chemicals in foliage.

If drought frequency changes as a function of altered precipitation, temperature, or both, trees and forests may become chronically stressed, leading to progressive deterioration in tree health and increasing susceptibility to secondary organisms and decline diseases. Pathogens could spread into new areas where they are presently limited by low temperature. Reproduction rates could increase, increasing disease severity and accelerating the evolution of new pathotypes.

Lessons from the Past and Uncertainty for the Future

Changes in the distribution of vegetation are strongly correlated with climatic change over long periods, thus it is reasonable to expect that future climate changes will affect forest composition and distribution. Specific biological factors that affect species response to environmental changes include survival, reproductive capacity, rate of migration, and response variation between or within species. Anthropogenic stressors are a relatively new set of factors that affect evolutionary responses to changing environment.

Most modern vegetation assemblages have been in their present configuration for no more than 6000 to 8000 years. Present vegetation communities are transitory combinations of species that have responded individually to environmental changes and competition. Eastern white pine is an example of a species whose distribution has closely followed climate changes of the last 10,000 years.

Regression tree analysis on trees has been used to indicate prospective responses of individual species which are then aggregated to examine potential changes in community dynamics and biodiversity. Under climate change scenarios, balsam fir and quaking aspen were mostly lost from northern U.S. forests, and maples were greatly reduced. Pine species, primarily loblolly pine (*Pinus taeda* L.) and eastern white pine (*Pinus strobus* L.), expanded their dominance in the southern and northern parts of the region, respectively. Oaks (*Quercus* spp.) also expanded in some areas.

Both paleoecological studies and modeling efforts have clearly shown that vegetation communities are unlikely to move together as intact communities. Consideration of additional factors that contribute to the uncertainty of prediction only strengthens this general conclusion. For example, the determinants of the boundaries of the current distribution of any particular species are poorly known. Anthropogenic factors, such as exotic species introductions, changes in land use, and forest management, also play a role in conjunction with changing environmental factors.

There are differential responses to environmental change between species and within species, as shown by numerous experimental studies. For example, eastern white pine is highly sensitive to air pollution, with many of the sensitive individuals already lost from natural populations. Greenwood and Hutchison (1996) showed that temperature during breeding can have effects on the genotype and phenotype of progeny even if identical parent material is used. They observed significant growth differences as a function of crossing environment.

Most natural populations of temperate and boreal species seem to be quite tolerant of climate differences as indicated by a long history of provenance testing. In the northern U.S., most species should tolerate climates as much as 5°C warmer than present, as long as other factors, such as moisture availability, do not change simultaneously. However, regeneration in the face of climate change is

likely to be more difficult than survival, because the most sensitive stage of a tree's life is the beginning, when warmth and drought can have strong effects.

Species migration is dependent on regeneration success. Other factors are also important, such as nonnative tree species and their competition effect, or forest fragmentation, which may be a barrier to migration.

The Potential Effects of Global Change on Northern U.S. Forests

Ecosystem responses to changes in multiple environmental factors are exceedingly complex and cannot be predicted with certainty using current experimental results and models. Environmental factors known to cause changes in ecosystem processes include climatic variables, tropospheric O₃, N deposition, acid deposition, and anthropogenic factors such as past land use and introduction of exotic species. Experimental studies can logistically include controls for only a few of the important factors governing ecosystem processes. Observational studies lack control for establishing definitive cause and effect relationships. Models lack sufficient mechanistic detail and input data, and are often not validated for regional applications. However, there is some knowledge to be gained from each approach, and when the different approaches begin to converge by indicating similar ecosystem responses, we can be more certain about conclusions.

Some Significant Findings

Evidence from experiments that address combinations of factors has shown:

- Elevated CO₂ usually increases tree biomass growth, while exposure to elevated and ambient O₃ usually decreases biomass growth. Controlled exposure of trembling aspen to both elevated CO₂ and O₃ shows that elevated CO₂ may not compensate for reduced growth caused by elevated O₃ in sensitive genotypes. When N is limiting, there may be a “smaller positive growth response to elevated CO₂.”
- Because CO₂ and O₃ change the chemical composition of the foliage, resistance to insect attack and nutritional value of foliage are altered. Elevated O₃ appears to increase insect growth and elevated CO₂ decreases insect growth.
- It is likely that increased winter injury to red spruce is the result of acid deposition and altered weather patterns. The strongest evidence for an environmental effect on incidence of freezing injury is that exposure to acid cloud water increases the risk of foliar freezing injury by reducing the cold tolerance of current-year foliage by 5 to 12°C. Recent research has pointed toward a mechanism of acid-induced loss of calcium from cellular membranes.
- Watershed-scale additions of N at both Bear Brook in Maine and Fernow Experimental Forest in West Virginia have clearly shown that the majority of deposited N is retained in ecosystems that have experienced chronic N addition. There is no conclusive evidence that increased N resulted in increased vegetative growth. Although most fertilizer trials shown an increase in growth, at least two experiments with conifers show reductions in growth from chronic N additions.
- Experimental evidence supports the hypothesis that an increase in soil temperature of 1.0 to 3.5°C can have significant effects on belowground C and N cycling in northern U.S. forests. Soil respiration and N mineralization showed significant and consistent increases regardless of site or treatment. Oxidation of methane, nitrous oxide flux, and litter decomposition showed variable responses that depended on litter quality, N availability, and soil moisture.

Observational studies have shown strong correlations between some environmental factors and responses:

- Acidic deposition lowers the pH of the mineral soil, causing mobilization of Al that can then be transported into the forest floor, reducing the amount of available Ca. The Ca/Al molar ratio of the soil solution seems to be related to the mechanisms by which acidic deposition affects forest growth and is an important indicator of potential stress.
- The direct effects of warming on insect physiology are likely to increase the frequency, level, and geographical extent of disturbance by insect pests. The effects of warming may be mediated by changes in feeding behavior brought about by the exposure of foliage to elevated O₃ and CO₂, which alter the nutritional value of the foliage.
- Most natural populations of temperate and boreal tree species seem to be quite tolerant of climate differences as indicated by a long history of provenance testing. In the northern U.S., most species should tolerate climates as much as 5°C warmer than present, as long as other factors such as moisture availability do not change simultaneously.

Integrated modeling studies and model comparisons suggest that:

- Estimates of the effects of ozone on annual net primary production of hardwood forests at the regional scale range from no effect to 17% decrease in productivity. Productivity reductions are more likely to occur where both ozone levels and stomatal conductance are greatest.
- It is likely that the combined effects of increased atmospheric CO₂ and projected climate change will increase forest productivity. Uncertainty in this conclusion is related to the high uncertainty in the projected effects of increasing greenhouse gases on precipitation. An increase in temperature accompanied by a decrease in precipitation could cause plant stress and a reduction in NPP. The magnitude of the water stress would be ameliorated to some degree by CO₂-induced stomatal closure, which increases water use efficiency.
- Regression tree analysis of composition changes suggests that under warming scenarios, balsam fir and quaking aspen were mostly lost from northern U.S. forests, and maples were greatly reduced. Pine species, primarily loblolly pine and white pine, expanded their dominance in the southern and northern parts of the region, respectively. Oaks also expanded in some areas.

Two or more lines of evidence coverage in supporting the following statements:

- Numerous experimental and observational studies have shown major differences in the response of species and genotypes to multiple interacting environmental factors.
- Both paleoecological studies and modeling efforts have clearly shown that vegetation communities are unlikely to move together as intact communities.
- Experimental research and models suggest that exposure to ambient levels of O₃ may damage sensitive plants, causing growth losses under conditions conducive to damage such as during high water uptake.
- Northern U.S. forests have sequestered a significant amount of C over the past 50 years, and are expected to continue sequestering C unless affected by natural and human-induced disturbances that far exceed recent levels.
- Because of the complexity of soil process responses, it is not possible to definitively state whether Northern U.S. forest soils will be a net source or sink of C as a consequence of atmospheric

warming. However, the balance of experimental evidence and observations suggests that warming of northern temperate forests will result in a net efflux of C from the soil to the atmosphere.

The effects of many environmental changes on forest productivity and health are mediated through changes in soil process:

- Depletion of base cations has been identified as a critical issue for northern forest soils. If weathering of parent material is not sufficient to replace base cations lost to forest growth and leaching, then depletion is likely. It has been clearly established that acidic deposition can decrease nutrient retention in forest ecosystems and cause imbalances in the availability of nutrients.

Human factors underlie some of the observed changes in forest ecosystems:

- Land use history is among many factors such as vegetation type and soil characteristics that affect the susceptibility of a forest site to N saturation.
- Anthropogenic stressors are a relatively new set of factors that affect evolutionary responses of trees to a changing environment. Some influential anthropogenic factors include exotic species introductions, changes in land use (and forest fragmentation), and forest management.

Vulnerable Northern Forests

Northern forests have heretofore shown remarkable resiliency and adaptability despite high levels of environmental stress. We have documented climate trends, ozone exposure, high levels of acid and nitrogen deposition, and land use pressures, all simultaneously affecting northern forests. Yet northern forests appear healthy as a whole despite evidence of local problems, and regional inventories continue to show accumulation of biomass and low (though increasing) mortality. Evidence suggests that decades of stress may have altered long-term soil processes sufficiently to begin affecting regional indicators of health and productivity. Therefore, an increased level of monitoring, targeted to areas suspected to be sensitive to environmental change, is warranted.

Forest ecosystems that appear vulnerable to past or continued environmental stress include:

- Northern Red Spruce Forests—These forests are damaged by acid deposition and winter injury and are vulnerable to additional climatic stress. Winter injury, common when temperatures fluctuate broadly and when foliage is damaged by acid deposition, could become more common. High-elevation spruce-fir forests in the middle Appalachians are remnants of an earlier, cooler climate now found only at the highest available elevations.
- Aging Hardwoods in the Mid-Atlantic Region—If the theoretical models are correct, then increased levels of various interacting stressors in the Northeast are likely to lead to increased incidence of decline disease. Increasing environmental stress is occurring at the same time as many species reach biological maturity across much of their range, a consequence of past land use impacts. Aging forests are known to be more susceptible to decline disease. Vulnerable types include maple-beech-birch, oak-hickory, and black cherry in Mid-Atlantic States. Mid-Atlantic forests are exposed to high levels of O₃ and acid deposition, and as they age, are showing increased mortality typical of mature forests. For example, mature sugar maple on unglaciated soils in northwestern Pennsylvania are noticeably affected by biotic factors (defoliating insects, borers, and canker fungus),

a series of droughts, and acid deposition. Regeneration of some aging forests is very uncertain. Lack of oak regeneration following harvest is considered a major issue for the region, as loss of oak forests coupled with a major expansion of red maple results in lower economic value and reduction of important mast species. However, regeneration in the face of climate change is likely to be more difficult than survival, because the most sensitive stage of a tree's life is the beginning, when warmth and drought can have strong effects.

- **Aspen-Birch in the Lake States**—Aspen-birch forests in the U.S. grow at the southern end of their current range. Aspen is sensitive to O_3 , and for some genotypes, CO_2 benefits are not sufficient to offset the negative effects of O_3 . It is unknown how climate change might alter aspen-birch forests when coupled with these physiological responses. Over North America, the most significant observed temperature changes over the last 40 years have occurred from the north central U.S. through northwestern Canada into Alaska. Thus, it is possible that multiple stresses will converge on aspen-birch forests in the Lake States with unknown but potentially harmful consequences.

Protecting the Values of Northern Temperate Forests

Northern temperate forests are important components of earth's terrestrial ecosystems and help regulate the concentration of atmospheric CO_2 . Maintenance of these forests in a healthy and productive state will ensure their continued role as reservoirs of C that could otherwise be released and exacerbate the global problem of increasing atmospheric CO_2 . Northern forests contain large reservoirs of C, particularly in abundant maturing forests and forest soils. Northern U.S. forests contribute an estimated two-thirds of the total U.S. accumulation of C in forest ecosystems, which helps offset emissions from fossil fuels (Birdsey and Heath, 1995). Although this rate of accumulation may slow as the forests continue maturing (Figure 1), it is nonetheless important to maintain healthy forests and avoid large future releases of CO_2 from forest biomass or soils.

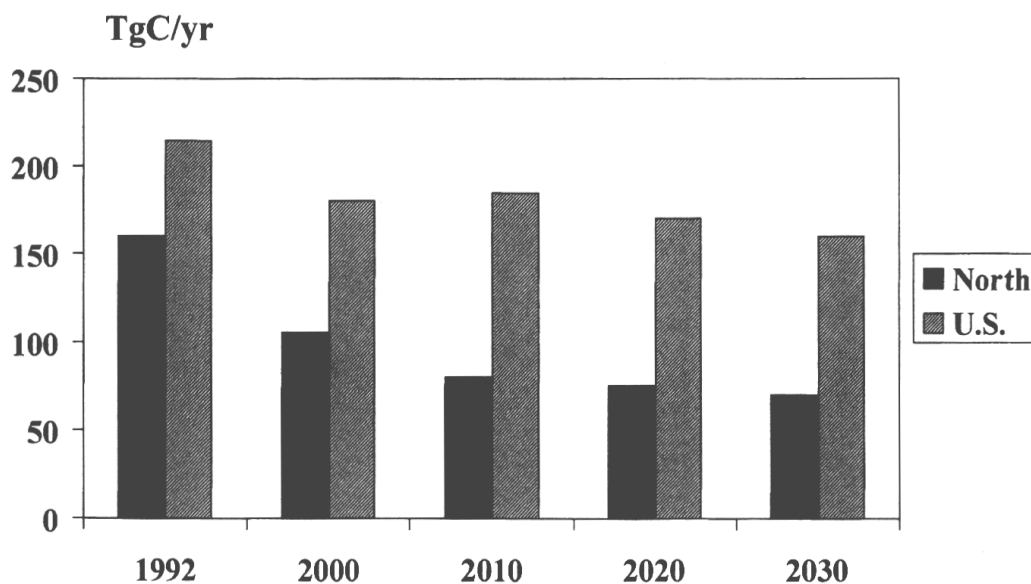


Figure 1. Projected periodic average annual carbon uptake (million metric tons yr^{-1}) in northern and all U.S. forests.

Long-term productivity and C storage of forests in the North are threatened by acid deposition (Adams, 1999; Hornbeck et al., 1997). Acid deposition affects cation availability and nutrient cycling in a variety of ways depending on soil parent material, management history, and other controlling factors. Forest managers will increasingly be required to monitor soil characteristics to sustain forest values over the long term.

Forests protect water supplies by keeping soil in place and reducing reservoir siltation, by absorbing pollutants and regulating the release of pollutants, and by regulating the discharge rate of water. Because of the proximity of Northern forests to great population centers, their value in protecting water quality and quantity is very significant. For example, the Catskill Mountains, nearly 100% forested, provide water for residents of New York City that is clean enough to be supplied without treatment.

Many northern forests provide timber for economic uses, recreation opportunities for residents and tourists, and wildlife habitat. Only a few of the many forest values that are potentially affected by climate change have been studied, but those that have show a variety of significant positive and negative responses. For example, a study of the potential effects of warming on brook trout in the Central Appalachians suggests that as stream temperature increases, trout growth increases in the spring and decreases in the summer; habitat is reduced; and predator abundance could increase (Ries and Perry, 1995). Knowledge of these potential effects would help sustain forest values and maintain the stability of dependent human communities.

Genetic and phenotypic variability is fundamentally important to survival on a changing planet. Maintaining and protecting sufficient natural variability within tree populations is thus critical for future evolutionary adaptation and maintenance of health and stability within northern forests. Perhaps the greatest anthropogenic threat to northern forests is the combination of unprecedented climate change, pollutant exposure, and degradation of genetic diversity needed for adaptation and survival.

Mitigating Climate Change Through Forest Management

By signing the Kyoto Protocol in 1998, the U.S. government reaffirmed its commitment to meet the challenge of climate change by reducing greenhouse gases. Under the terms of the agreement, the U.S. must reduce net emissions 7% below 1990 levels by the first reporting period, 2008 to 2012. Although the exact terms that will be used to implement the protocol are still under discussion, there will be some opportunity for land use change and forestry activities to contribute to greenhouse gas reductions if it can be shown that these activities increase the size of the terrestrial C sink. The increased C sequestration should be relative to an average baseline that would occur in the absence of the activity.

It is relatively easy to show that conversion of nonforest land to forest land (afforestation) causes an increase in sequestered C, and that conversion of forest land to nonforest land (deforestation) causes a decrease in sequestered C. Because the North is already heavily forested and land use change affects a small proportion of the land base, it is likely that changes in forest management, which could affect large areas, would have the greatest impact on reducing atmospheric CO₂.

Forest inventory data for the North show that the region's forests currently sequester C at an average rate of 2.3 t ha⁻¹ yr⁻¹ (Birdsey and Heath, 1995). Even unmanaged, aging forests in the North continue to accumulate C at a high rate. For example, Johnson and Strimbeck (1995) measured the change in biomass and soil C over a 33-year period for 23 stands of aggrading sugar maple in Vermont, ranging in age (at initial measurement in 1957 to 1959) from 47 to 97 years. They found that only 2 stands lost biomass whereas 21 gained biomass. The average gain in biomass for all stands was

1.8 t ha⁻¹ yr⁻¹. There was no detectable change in soil C over this period. Another study used the eddy covariance technique to directly measure the exchange of CO₂ in a 60-year old northern hardwood ecosystem in Massachusetts (Wofsy et al., 1993). They estimated a significant net C sink of approximately 3.7 t ha⁻¹ yr⁻¹.

Much higher rates of C sequestration are possible in forests that are managed for biomass production. The average C storage in biomass (including cut and dead trees) for 40-year old hardwoods in the Lake States under different management intensities was 331 Mg ha⁻¹ (Strong, 1997). This is equivalent to an average annual C accumulation of 8.3 t ha⁻¹ yr⁻¹. There was a small effect of harvesting on soil C, with heavier cutting reducing soil C by 25% compared with the control (no treatment) which had 120 Mg C ha⁻¹. Another study showed that conversion of cropland to fast-growing hybrid poplar caused a significant gain in soil C after about 10 years (Hansen, 1993). Soil C accretion beneath 12- to 18-year-old poplar plantations exceeded that of adjacent agricultural crops by 1.6 Mg ha⁻¹ yr⁻¹.

Carbon from forests can remain stored in forest products long after forests are harvested and the wood processed into products. Carbon stored in trees harvested in the early 1900s still remains stored in wood of houses built from this wood. It is estimated that the accumulation of C in wood products and landfills from harvested northern forests totals approximately 0.015 Pg C yr⁻¹ (Heath et al., 1996).

Urban and suburban forests may play a significant role in sequestering carbon through tree growth and energy conservation. A study of Chicago's urban forests found an average of 14 to 18 t ha⁻¹ of C in tree biomass (Nowak, 1994). Urban trees also reduce the use of energy for heating and cooling, thus avoiding CO₂ emissions.

The need to protect forests from fire, pests, and other stresses is important both to secure the role of forests in mitigating climate change and for avoiding adverse impacts of climate change and air pollution. Forest managers need to be aware of threats to forest health and productivity that may not be too obvious and take adaptive actions as necessary to sustain the many values provided by northern forests.

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