

Climate Change and Forest Dynamics: A Soils Perspective

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ABSTRACT

Increasing temperatures have been recorded around the world, leading to changes in precipitation, sea-level rise and extreme events. Climate models are currently in use to simulate the effects of these changes on vegetation cover, which is a strong indicator of ecosystem changes in response to various drivers. Climate change, as well as anthropogenic stressors, is affecting forest dieback and tree-species migration. This chapter addresses the connections between changes in various forest types and the global soil carbon, nitrogen and hydrologic cycles, and related feedbacks between these factors and both natural and anthropogenic environmental changes. We discuss the ways these feedbacks between land use, vegetation changes and global nutrient and water cycles can lead to further climate change and soil degradation, which have profound effects on food security, and we conclude by proposing the use of soil characteristics as tools to inform land managers of challenges they may face in preserving valuable services from forested lands and cropping systems.

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1 Introduction

Widespread forest mortality is a worldwide phenomenon, and scientists researching possible causes often arrive at the conclusion that effects of climate change are behind much of the forest dieback.^{1,2} In the past two decades, warmer temperatures and decreased precipitation have been identified as the main causes for pest outbreaks, increased forest fire frequency and extended drought-related stress.^{3,4}

Climate change is an important factor leading to forest dieback and tree species migration as they relate to drought, water stress, early snow melt, reduced snow cover, pest outbreaks and fire risk.^{1,2,5,6} Forest ecosystems are facing many stresses, both natural and human-caused that can contribute to changes in forest dynamics. Anthropogenic stressors are often related to land conversions for agriculture or urbanisation, fire suppression or initiation, and pollution. Natural stressors may include severe drought, waterlogging and cold, and secondary insect attacks and diseases of stem and root fungi.⁷ Although some forests might have a positive response to increased carbon dioxide emissions and longer growing seasons,^{8,9} this response appears to be regional or temporary as current global forest loss is exceeding forest gain¹⁰ (Figure 1).

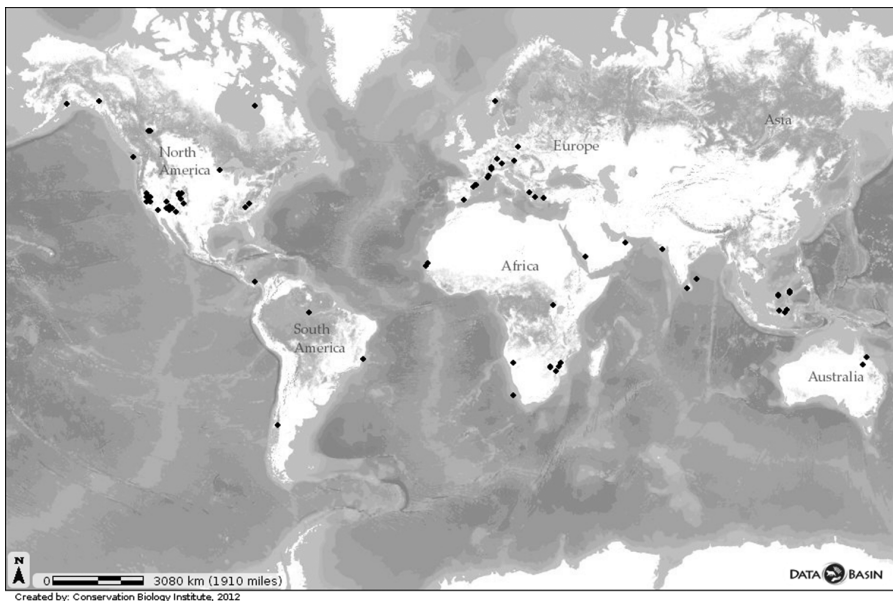


Figure 1 This map shows the locations of forest dieback documented in a 2010 publication.² An interactive version of this map, including details of forest type, dieback causes and extents and original data sources can be found at: <http://app.databasin.org/app/pages/datasetPage.jsp?id=b2947eeae2e5488a86eacf0fcd4df7a4> (Source: Dr. Joerg Steinkamp, Biodiversity and Climate Research Centre, Wendy Peterman, Conservation Biology Institute).¹¹

Due to limitations in the understanding of forest physiology, climate and mortality, forest die-offs are a big uncertainty in climate projections of terrestrial ecosystem impacts, climate/ecosystem interactions and carbon-cycle feedbacks.¹² Scientists are always seeking greater understanding of the complex mechanisms leading to forest dieback, migration and shifts in species dominance to help predict where and when these changes may occur.

Soils hold important clues about shifts in hydrology and vegetation across the landscape because, in terrestrial systems, soil characteristics govern the reception, storage and redistribution of precipitation. This, in turn, determines the supply of plant-available water and, indirectly, the nutrients necessary for plant establishment and growth. Because soils with more water are less sensitive to warming, changes in soil moisture result in changes in soil heat capacity and conductivity, which, in turn, affect infiltration and water transport in the soil profile.^{13,14} Soil response to changes in precipitation has implications for vegetation water needs, fire risk, pest outbreaks, infiltration rates and groundwater recharge;¹⁵ therefore, in-depth analyses of these soil characteristics can give scientists and managers the tools they need to predict where trees will be most vulnerable to future water stress and where they will be most likely to establish and thrive under future conditions.

In this chapter, we review existing literature for examples of on-going forest responses to climate change, many of which are also exacerbated by anthropogenic stressors. We discuss the implications for the global carbon, nitrogen and hydrological cycles and how resulting changes in forest lands and associated ecosystem services may affect food security in the future. We conclude by providing a method to use soil characteristics to inform land managers of challenges they may face in preserving valuable services from forested lands and cropping systems.

2 Projected Trends in Climate Change

2.1 General Climate Trends

Rising temperatures have been recorded around the world and are projected to continue to rise, with regional and local patchiness, causing an overall decrease in the longevity, extent, and thickness of glaciers, ice sheets, and snowpacks.¹⁶ Observations have shown that land has been warming up at a faster rate than oceans, due to the greater inertia of deep oceans. Sea-level rise projections presented in the last IPCC report² were extremely conservative, and new publications suggest that higher levels are likely to be reached by the end of the century, if current trends of ice-melting and ocean-warming continue.¹⁷

Global warming is likely to drive an increase in global mean precipitation (rain and snowfall). However, the degree of spatial and seasonal variation remains large, even when considering multi-model means. All simulations point to increases in precipitation at high latitudes where more rain than snow has recently been observed, a trend that probably will continue as winter

temperatures increase. There is also a general agreement over precipitation decreases in the sub-tropics. Models agree to a lesser extent over an increase of precipitation in the tropics, and cloud formation and wind patterns are areas of uncertainty in model structure, as current understanding remains limited.

Natural climate variability (*e.g.* El Niño Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO), Atlantic Multi-decadal Oscillation (AMO)) and its impacts have been well documented for many regions of the world,¹⁸ but the understanding of the causes of shifts in teleconnections (related climate anomalies) remains limited and thus difficult to include in climate models.

Extreme events (long, intense droughts, flood, hurricanes and typhoons) are also difficult to predict from general circulation models. The latest report from the Intergovernmental Panel on Climate Change (IPCC)¹⁹ warns about the increased risk of more intense, more frequent and longer-lasting heatwaves, as exemplified by the European heatwave of 2003 that killed several thousands of people and caused widespread forest mortality.²⁰ Along with a greater risk of drought, there is an increased chance of intense precipitation and flooding due to the greater water-holding capacity of a warmer atmosphere, such that both wet and dry extremes should become more severe. Several modelling studies are projecting that future cyclones could become less numerous but more severe, with greater wind speeds, more intense precipitation, and higher ocean waves.

These extreme events, while unpredictable, often shape our landscapes. Past extreme events such as the drought of the 1930s that caused the Dust Bowl in the USA, or the 1998 floods in China caused by heavy rainfall that affected 240 million people, certainly affected natural ecosystems and human land use. Recently, reports of extreme events have been increasing. For example, a drought in the of summer 2010 caused crop failure and huge fires in Russia, while record rainfall caused extensive flooding and loss of life in both China and Pakistan. These extremes might be evidence of climate destabilisation, but they are at the very least consistent with what climate scientists have been expecting. They certainly pose a challenge to the more comfortable prospect of chronic linear change rather than abrupt and unpredictable change, yet these events might be what people most need to take into account when they consider preparing for change. In the past, the reliability of models was tested in part by simulating large disturbances and observing the simulated system's response. It may be necessary for practitioners to focus on disturbance simulation to fully explore the resilience of their systems.

3 Changes in Forest Dynamics

3.1 Introduction

Forests and woodlands account for approximately 30% of terrestrial land cover²¹ and store about 45% (more than 1 trillion tonnes) of the carbon in terrestrial ecosystems.^{12,22} Changes in vegetation cover are strong indicators of

ecosystem changes in response to many change agents, including land use and climate change. Forests can be either contributors or inhibitors of climate change on regional scales, but they have the potential to play a significant role in mitigating the pressures of global environmental change.²²

Land-use practices and climate change may work in concert to weaken the ability of trees to defend themselves against pests, improve conditions for native pests to flourish, and introduce unfamiliar pests to new locations. Non-native forest pests have increased globally since the 1990s due to increased international trade and other human activities²³ and now threaten forest productivity and diversity.^{24–27} For example, the root fungus *Phytophthora cinnamomi*, which originated in Papua New Guinea and is now contributing to forest mortality in the USA and Australia, and to Iberian oak decline in the Mediterranean and coastal northwestern regions of Europe,⁷ is a pathogen requiring warm, wet soils to infect roots, and extreme weather conditions, such as drought or waterlogging, can increase the susceptibility of trees to infection.⁷

In addition to non-native pest introduction, pollution is another human cause of altered forest dynamics around the world. Forests adjacent to urban and agricultural areas are responding to increased nitrogen deposition and other airborne pollutants.^{28,29} Human activities such as road-building and land conversion lead to landscape fragmentation, which increases forest edges.²⁹ These edges can be “hotspots” of dry deposition, with as much as four times the rate of atmospheric nutrient delivery as areas without edges.^{30,31} The difference between pollutant concentrations from the forest edge to the interior can be very large, possibly even exponential, especially when particles are transported horizontally by wind.²⁹ Several studies of excessive nitrogen deposition have shown that the cumulative effects of nitrogen additions over many years can be negative due to a phenomenon called “nitrogen saturation”,³² which can ultimately lead to nitrogen leaching into surface waters.³³

3.1.1 Tropical Peat Swamp Forests

Montane peat swamps in cloud and other tropical forests play a significant role in the global carbon cycle as they store a considerable amount of carbon in their soils.^{34,35} Approximately 60% of the known peatland forests are in south-east Asia. Peat soils form from decayed woody plant debris decomposing in high precipitation and temperature conditions in swamp forests at low elevations in river valleys.^{36,37}

A high estimate of the remaining historical peat swamp forests is 36%.³⁸ Drying of peat swamps through logging or for agricultural use is increasingly common, but when these soils dry, they are extremely flammable.^{39–41} Peat soils are unique in their ability to burn above and below ground.⁴² Clearance and burning of peat swamp forest in south-east Asia could contribute to 3% of total global human emissions.^{43,44} The 1998 Indonesia fires burnt some 8

million hectares of land and, according to scientific estimates, released between 0.48 and 2.57 Gt of CO₂ into the atmosphere, which is between 13 and 40% of the mean annual global carbon emissions from fossil fuels. The exact amount remains uncertain.⁴⁵

3.1.2 Tropical Rainforests

Changes in Amazon rainforest ecosystems have the potential to affect not only the global carbon budget, but the hydrological cycle and feedback to global climate as well. Climate and air quality in the Amazon region are highly dependent on feedbacks between vegetation cover, land surface and biogeochemical fluxes.⁴⁶ Approximately eight tonnes per year of water evaporates from Amazon forests.¹⁹ Run-off from the Amazon basin to the Atlantic Ocean accounts for 15–20% of the global freshwater flow to oceans.⁴⁷ Amazon forests also contain currently between 90 and 140 billion tonnes of carbon,⁴⁸ which is about nine-to-fourteen decades of the current anthropogenic carbon emissions.⁴⁹

Some simulations indicate Amazon forests will convert to grasslands by the end of the 21st century,^{50–54} causing dramatic changes in soil and hydrologic conditions.⁵⁵ The HadCM3 general circulation model projects that regional warming and drying will also lead to large-scale forest dieback.⁵⁶ Grasses can expand into disturbed forest patches *via* animal or wind seed dispersal, but more often there is deliberate grass seeding by ranchers after logging.⁵⁷ As of 2001, deforestation in the Amazon had reduced the original forest area from 6.2 million km² to 5.4 million km² (*i.e.* 87% of original area),⁵⁶ and existing plans to build new infrastructure could further reduce Amazon forests to 3.2 million km² (53% of original) by 2050.⁴⁸

The overall indications of research on Amazon forest decline is that forest degradation by humans or climate could lead to an even hotter, drier climate in Amazonia. Deforestation reduces the recycling of water,^{44,55} while decreased forest evapo-transpiration leads to decreased surface cooling, which leads to warmer air temperatures, higher evaporative demand and increased water stress.^{55,56} Fire hazard also increases in a drier climate, potentially causing an increase in smoke and dust aerosols that could alter the frequency and amount of precipitation received.^{55,58} A coupled climate-carbon model from the UK Meteorological Office Hadley Centre showed that severe drying of Amazon forests would lead to forest losses, resulting in feedbacks at both regional and global scales, further magnifying drought conditions and forest degradation.^{46,56,59}

Amazon forests on dry margins or on shallow, infertile soils are most vulnerable to drying.⁵⁵ Amazon trees avoid drought stress by penetrating deeply into the soil to access deep soil water, and they utilise hydraulic redistribution of water to more shallow soil horizons.^{60–64} The threshold of drought tolerance in Amazon forests has been shown experimentally as an available soil water capacity less than 30% of its maximum value.^{62,65} During

the El Niño 1997–1998, forest mortality increased 50% post-drought⁶⁶ as canopy dieback increased radiant energy into the forest and increased the temperature in the forest interior, further drying the soils and increasing fire risk.^{57,67}

In addition to climate change, human pressure on Amazonia is important. Humans look to this region to exploit biofuels to substitute for oil, cattle and swine industries, agro-industry expansion, sugar cane for ethanol, palm oil for biodiesel and soy crops.^{55–57} Land-use changes increase habitat fragmentation, edge effects of pollution and dry air circulation under forest canopy, and fire ignition sources.⁵⁷

3.1.3 Temperate Forests

In the USA, the regional importance of many tree species is changing rapidly. Some tree species are experiencing dieback in response to precipitation and temperature changes, while others are seeing shifts in species dominance. In a regression tree analysis of eighty common trees species under five future climate scenarios for 2100 counties in the eastern USA, Iverson and Prasad⁶⁸ project that average species richness may remain the same or even increase with climate change, but there are likely to be dramatic changes in forest type in this region.

All five models⁶⁸ predict an extirpation of spruce-fir forests in New England, USA, and all but the two least-severe models show an extirpation of aspen and birch species (both still largely reduced). Maple, beech and birch species are largely reduced under all scenarios. The main increases are seen in oak-hickory and oak-pine woodlands, which are projected to increase 34% and 290%, respectively. The loblolly shortleaf pine is projected to decrease by 32% and shift its range to the north and west. Longleaf slash pine is projected to decrease by 31%, but elm-ash-cottonwood woodlands are projected to remain in the upper Great Plains region of the USA.

According to their consensus models, 24 species in the eastern USA will see a decline of at least 10%, while 35 species will see an increase in regional importance, with 12 of these increasing by 100% or more. Recent national forest assessments²¹ indicated that the total area of USA national forests has been increasing annually, but that the amount of increase is slowing dramatically. More recent US Forest Inventory Analysis (FIA) studies⁶⁹ show that some eastern states are levelling off in forest increase and others are beginning to decline.

Coops and Waring^{70,71} used the 3-PG process-based model to predict forest responses to climate change. Predictions of future tree distributions in the Pacific Northwest of the USA show large changes in lodgepole pine and ponderosa pine distributions. They show that lodgepole pine is most likely to persist at sites with significant spring frost, summer temperatures below 15 °C, and soils that are fully recharged from snow melt. Using future climate projections, they predict a decrease of 8% in suitable lodgepole pine habitat

and, by the last 30 years of the 21st century, they predict that the species will be absent from most of its current range. By 2050, there is likely to be a significant decrease in its distribution, especially in central Oregon and Washington, British Columbia and the western side of the Rocky Mountains, so that by 2080 lodgepole pine is projected to be gone from Oregon, Washington and Idaho (Figure 2). The most restricting factor in the pine persistence is soil water.

As the climate warms, tree species are expected to migrate to higher altitudes and higher latitudes into areas previously characterised by low temperatures. The compositions of high-elevation forests are changing rapidly.¹⁵ Altitudinal tree lines are seen as the most sensitive to global warming, because historic temperature decreases at higher altitudes have been the main limitation on tree lines globally.⁷³ As temperatures increase, altitude becomes a less reliable predictor of tree-line limitation. In the Andes, Chile, Patagonia and the Rocky Mountains of Montana, tree growth at tree lines did increase in brief pulses with subsequent infilling over several centuries, but, in the past fifty years,

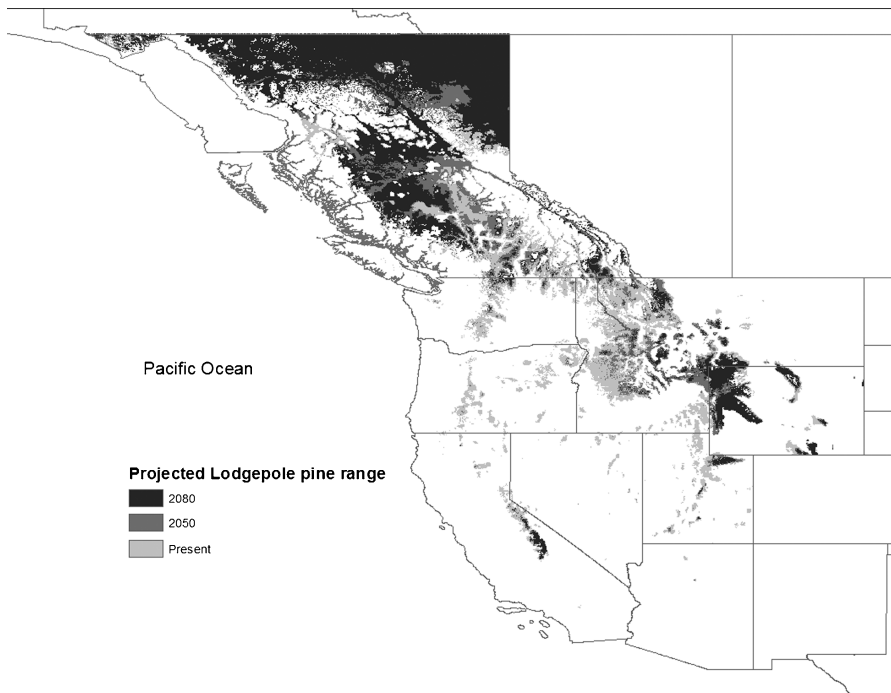


Figure 2 This map shows the lodgepole pine (*Pinus contorta*) projected range contraction in North America between the present and 2080.⁷² (An interactive version of this map and other maps of future species distribution simulations can be found at: <http://app.databasin.org/app/pages/galleryPage.jsp?id=896ee1c381fd4a50b5f811b4b11c0898>).

these regions have shown actual declines at the tree line, with the biggest decline 200 m below the tree line.⁷³

Although many species have been observed to move uphill in response to temperature, this change alone is not enough to understand future plant distributions. There is evidence of some downhill shifts despite climate warming.^{74–76} Drivers of species distribution shifts and mechanisms are not well understood at present, but it's possible that some species may track decreases in water deficit to lower elevations rather than temperature increases to higher elevations.⁷⁷ In the past century there has been an increased density of younger tree cohorts at lower elevations.^{78,79}

3.1.4 Alpine Forests

Climate projections show the greatest and earliest warming trends at higher latitudes (45 to 65 °N), especially in continental interiors.^{80,81} At the thermal ecotone, small changes in temperature can have large consequences.⁸² The interior regions of Alaska are good places to investigate possible climate-change effects on vegetation composition and soil thermal dynamics, because changes in snowmelt affect surface and sub-surface soil moisture through interactions with permafrost.⁸³ Changes in surface hydrology and soil temperature affect forest and tundra vegetation as well as forage availability for ungulates.⁸⁴ In Alaska, the tree line is shifting northward into the tundra, important migratory bird and caribou habitat.¹⁵

Yellow cedar (*Callitropsis nootkatensis*), a tree found in British Columbia, Canada, and the Pacific Northwest of the USA, is experiencing varied responses to changes in soil temperature and hydrological conditions.⁸⁵ Between the 19th century and the present, yellow cedar has seen a high rate of mortality only in SE Alaska and bordering regions of Canada, with dieback symptoms originating in the roots, spreading to the crown and finally manifesting in the bole of the trees.⁸⁶ The emergence of the initial symptoms in the roots indicates soil factors in the causes of stress,⁸⁵ which generally makes trees more susceptible to predators; however, biotic agents are not the primary cause of death.^{87–93}

Yellow cedar is usually drought tolerant and successful in poor soils,⁹⁴ but it also tends to decline on poorly-drained soils,⁸⁷ and in the late 19th century a warming period at high latitudes⁹⁵ was associated with yellow cedar decline.⁹⁶ D'Amore and Hennon⁸⁷ explored the soil conditions connected to cedar decline and concluded that warmer air and soil conditions, reduced snow packs, and early spring warming are causing trees to de-harden too early and to become susceptible to late-frost injury.

3.2 Hydrologic Responses

Changes in temperature, precipitation and vegetation cover have major implications for the global water balance in which soils play an integral role.

One of the most valuable ecosystem services provided by forests at the watershed scale is to provide clean drinking water. With warming, there will be an increased need for forest cover to provide shade and reduce evaporation, protecting soils and streams from water losses, while potential declines in their extent due to human land-use or increased climate-driven mortality may reduce their ability to do so.⁹⁷ Although some studies have shown that forest harvest on certain soils with certain topography can increase water yields, particularly when precipitation exceeds evapotranspiration, this increase in water from vegetation removal is small and short-lived,⁹⁸ and it has the potential to increase the frequency of landslides, because root removal destabilises soils.

Furthermore, small changes in the proportions of winter precipitation *versus* snow can greatly alter seasonal stream flow throughout the year.⁹⁹ Simulations run by Tang and Zhuang¹⁰⁰ show that increased precipitation combined with earlier snowmelt and delayed snow onset, lead to longer snow-free periods in tundra and boreal forests, which could increase the growing season by up to three weeks during the 21st century. In Alaska, USA, higher temperatures over the last century have led to changes in the length of the growing season for terrestrial ecosystems,¹⁰¹ and increased evapotranspiration in response to warming is also leading to an overall decline in spring soil moisture.¹⁰²

In southeast Asia, “cloud” forests that take water from clouds to augment ground water and mountain streams, sometimes doubling the effective rainfall in the dry season and increasing total forest moisture inputs by 10%,^{103,104} are threatened by climate change as well as expanding infrastructure, forestry and agriculture. Currently, tropical montane forests cover about 92 million hectares (15% of tropical rain forests).¹⁰⁵ One half of the tropical montane forests can be found in south-east Asia (approximately 32 million hectares).¹⁰⁶ The biodiversity of native frogs, birds and mammals can be higher than in lowland tropical rain forests, making these habitats critical for conservation.^{107,108}

The cloud forests of Malaysia are declining 23% faster than lowland forests in the region.¹⁰⁹ Clearing for agriculture and cattle leads to pesticide and fertiliser contamination in surrounding watersheds, decreased water yields in highland streams,¹¹⁰ and severe soil erosion and stream sedimentation.¹¹¹ In addition to land conversion, commercial selective logging currently affects 1.1% of cloud forests globally (higher than other tropical forests).¹¹² Possible solutions to cloud-forest decline may be increasing protected areas to preserve intact ecosystems and integrating the forests into desired human uses through agroforestry and increased animal husbandry, and thus increasing land-use efficiency.¹⁰⁴

3.3 Carbon Responses

One of the most important ecosystem services that forests deliver is in their role as a large carbon sink. According to the US National Climate Assessment,¹¹³ if

one-third of the current croplands were converted to forests, the US carbon emissions could be reduced by as much as 10%. Carbon uptake depends on climate, disturbance and management legacy, age and type of the forests.¹¹⁴ While water availability limits productivity in semi-arid grass, shrub, woodland and dry forest ecosystems,¹¹⁵ at high latitudes where low temperatures limit water availability, early snowmelt and soil thaw initiate photosynthetic carbon uptake, and warming induces a longer growing season where radiation is the limiting factor.¹¹⁶ Soil properties limit the availability of both water and nutrients, potentially limiting plant growth. Soil texture, depth, salinity and topography have strong local influences on forest growth.^{117–121}

Soil organic carbon (SOC) pools may store as much as 90% of the carbon in terrestrial ecosystems¹²² but can also vary widely in response to woody plant encroachment (from -6200 g C m^{-2} to $+2700 \text{ g C m}^{-2}$).^{121,123–131} The increase in woody encroachment of grasslands and deserts during the 20th century has been attributed to a variety of factors, such as increased atmospheric CO_2 concentration, land-use change (grazing), climate patterns and fire suppression.^{132–134}

Woody plants influence SOC pool sizes, particularly beneath their canopies,¹³⁵ through litter accumulation; they can affect soil respiration and leaching (roots and microbes) and reduce erosion.¹²¹ Because of the greater rooting depths and higher root lignin content of woody plant species, soil carbon is generally higher in shrublands than grasslands^{122,136,137} and is accompanied by more resistant organic matter in deeper soil layers.^{138–141} Barger *et al.*¹²¹ showed that bulk density and clay content mediate the magnitude and direction of SOC changes with woody encroachment. Increases in bulk density are linked to low SOC, and carbon losses are associated with soils of bulk densities greater than 1.6 g m^{-3} . In the southern Great Plains, USA, SOC accumulation rates are three times greater in fine soils than in adjacent coarse soils,¹³⁶ and woody encroachment with higher SOC contents has been associated with a clay gradient.^{142–145}

3.4 Nitrogen Responses

Nitrogen availability is closely tied to the water cycle^{146,147} and it controls photosynthetic rates and thus forest productivity, as well as carbon allocation and resulting canopy development.^{148–156} Nitrogen can limit carbon uptake even when water is readily available, but when water is limiting, plants cannot take up available nitrogen unless they develop a symbiotic relationships with a nitrogen fixer.^{157–159} For this reason, the sizes of the soil carbon and nitrogen pools are good indicators of any change in the local soil nitrogen-supplying capacity.^{160–162}

Nitrogen dynamics are very much driven by the constant feedbacks from plant, soil and microbial interactions.¹⁶³ Tree species influence nitrogen cycles in different ways through root uptake, mycorrhizal associations, exudation and the chemical quality of plant litter,¹⁶⁴ and trees in the same climate with

different soil fertility can exhibit different rates of growth and above- and below-ground nitrogen accumulation patterns.¹⁶⁵ For example, root turnover and exudation provide a large carbon and nutrient source for soil microbial communities¹⁶⁶ which can generate rhizosheaths to enhance plant nutrient and water uptake by creating a beneficial microenvironment around the roots. Mycorrhizal hyphae can also allow plants better access to resources in the various soil layers beyond the tree canopy.

The age and land-use history of a forest determines overall nitrogen availability. Older, aggrading systems retain their nitrogen biomass in the soil, but disturbed systems lose nitrogen in large pulses, decreasing nitrogen mineralisation for plant uptake.^{167–169} When fires burn forest litter and understory, immobilised nitrogen in the biomass gets released to the atmosphere.^{170,171} Other forest nitrogen outputs include biomass loss from harvest, erosion, leaching and gaseous transfers.¹⁷²

Forests in humid temperate ecosystems are historically nitrogen limited, but Skeffington and Wilson³² published a new theory of forest “nitrogen saturation” in response to increased levels of atmospheric nitrogen deposition. When background nitrogen levels are low, temperate forests usually experience sub-optimal nitrogen availability, and nitrogen additions can enhance tree growth on very short-term intervals.^{173,174} Under conditions of elevated nitrogen deposition, there is the potential for forest nitrogen concentrations to exceed plant and soil uptake, leading to nitrogen losses from the system.^{33,163} Nitrogen saturation is characterised by increased nitrate losses from forest soils in spring snowmelt and soil water percolating below the rooting zone during the growing season.^{33,175} As negatively charged nitrate ions leave the soil, they combine with positively charged ions such as calcium and aluminum that leach as well, causing decreased soil fertility and increased acidity.³³ Consequently, excessive nitrogen concentrations add stress to forest ecosystems in temperate regions and may lead to decreased forest production and eventually decline, as nitrogen-saturated forests become net nitrogen sources rather than sinks.^{33,163} Furthermore, leached nitrate reaching streams affects water quality and has implications for nitrous oxide emissions to the atmosphere.

Nitrogen leaching is highly dependent on precipitation and snowmelt as well as the amount of water infiltrating below the rooting zone in the soil.^{176,177}

At the Hubbard Brook Experimental Forest in New Hampshire, USA, Bernal *et al.*¹⁷⁸ observed that a decline in snowpack is turning the soil into a massive nitrate sink. Repeated model simulations of the system suggest that two mechanisms of soil organic nitrogen storage are responsible for the observed decrease in nitrate export: (1) more nitrogen is being held in the soil as decreased snowpack reduces the water flow paths, allowing more opportunities for microbes and plant roots to immobilise nitrates, and (2) the gradual accumulation of nitrogen as the forest recovers from abrupt nitrogen losses due to past timber harvests, hurricanes or ice storms. There also

appears to be a small effect of the recent sugar maple decline on the change in nitrate export.

4 Food Security Implications of Forest and Soil Responses to Global Change

4.1 Anthropogenic Soil Degradation

Forest degradation and the resulting soil degradation are closely tied to the major issues facing world food production in the face of global environmental change. Because soil degradation is affecting crop productivity and contributing to malnourishment around the world,¹⁷⁹ improving soil quality is essential to maintaining life on earth.¹⁸⁰ Soil health is a high priority listed by the United Nations' Millennium Project hunger task force and the United States Department of Agriculture reports that decreasing degraded soils and increasing crop yields by 0.1% could reduce the number of starving people by 5% in a decade. Global hotspots of degradation include central and southern Asia, China, the Andes, the Caribbean, and the savannas of South America.¹⁸¹

In 1991–1992, the International Soil Reference and Information Center (ISRIC) developed a global database of human-induced soil degradation. Soil degradation derives from increasing pressure on land to improve living conditions, provide higher standards of living, or simply allow human survival. Five human causes of soil degradation are: (1) deforestation or removal of natural vegetation for agricultural use, roads, timber harvest or urbanisation, (2) overgrazing, (3) inefficient agricultural practices, (4) overexploitation of vegetation for domestic use, such as fuels and fencing (incomplete vegetation removal is insufficient to prevent topsoil removal), and (5) bio-industrial activities that lead to soil pollution.¹⁸¹

In a 2004 *Science* article, J. Kaiser¹⁷⁹ gave an overview of global soil degradation and its impacts on regional food scarcity. Soil degradation is given as the main obstacle to reducing hunger in Africa and the cause of the current devastation in Haiti. The previously forested landscape of Haiti has been severely denuded until only 3% of the original forest cover remains. At least one-third of the landscape has lost too much topsoil to be able to support crops. In the 1930s, the USA temporarily experienced a similar plight when a combination of poor land-management and drought contributed to a massive loss of topsoil in the midwestern states. In China, the Loess Plateau, the site of the fastest topsoil loss in the world, loses approximately 1.6 tons of loess each year, and some lands in the lower Himalayas have totally lost the capacity for food production. In sub-Saharan Africa, where farmers cannot afford fertilisers, and crop residues and animal excrement are used for fuel, soil fertility is quickly declining. In some parts of Africa, farmers traditionally rested fields, but now land constraints are too tight. In the Middle East and India, poor irrigation is leading to salinisation of soil, and in Australia the

eradication of some native plants is causing dramatic changes in local water tables, leading to salinisation of the topsoil. Desert expansion, driven by conversion of grasslands in the Sahel of Africa, Kazakhstan, Uzbekistan and northern China, has led to wind erosion and dust storms.

4.1.1 Mechanisms of Soil Degradation

Oldeman¹⁸¹ defined two categories of soil degradation: (1) the displacement of soil material by water or wind erosion, and (2) *in situ* soil deterioration through chemical or physical processes. Erosion or topsoil removal reduces soil fertility and may reduce crop rooting depths. Deforestation, overgrazing, and agriculture are the main causes of water erosion, because they expose soil to the direct impacts of rainfall, and wind erosion is almost always caused by a decrease in vegetation cover from overgrazing or the removal of vegetation for another use. Chemical degradation can be from loss of nutrients and organic matter (insufficient fertilisers, using poor soils, removal of natural vegetation), salinisation (from poor irrigation practices), acidification (from over application of fertilisers), or pollution (in industrialised nations with high population densities). Physical degradation includes compaction or sealing (from heavy machinery, low organic matter or high silt), waterlogging (from human intervention in natural drainage systems), or the subsidence of organic soils (drainage or oxidation of peat soils).

Soil chemical and physical weathering rates are driven by vegetation, temperature, and precipitation.^{181,183} This can be greatly intensified in areas where land use accelerates soil denudation, exposing more mineral surface area and rocks.¹⁸⁴ Bayon *et al.*¹⁸⁵ showed that chemical weathering of surface minerals due to intensified human land-use and forest clearing, rather than regional climate change, may have led to an abrupt vegetation shift from rainforest trees to savannas in Central Africa 3000 years ago. Records of past vegetation patterns show a great loss of primary forests as they were replaced by savannas and other pioneer species between 3000 and 2200 ago. At the same time, archaeological research shows that Bantu-speaking people migrated into the region and cleared forest for agriculture and iron smelting.^{186–191} This large-scale deforestation event may still influence current vegetation patterns in African rainforests.^{192,193}

4.1.2 Soil Degradation Implications for Soil Carbon and Nitrogen

Land erosion plays a significant role in global nutrient cycles. Soil organic carbon and soil nitrogen are both easily removed by wind and water erosion, which can lead to feedbacks to the atmosphere. Land cultivation leads to organic matter losses, directly affecting the soil chemical, physical and biological properties that affect crop production.¹⁹⁴ Khormali¹⁹⁵ showed that soil organic carbon and nitrogen in Iran are significantly depleted by increased water erosion from past deforestation. Vagen *et al.*¹⁹⁶ showed that some landscapes under cultivation more than fifty years without organic matter enrichment have

extremely low organic carbon and total nitrogen content. Soil carbon and nitrogen content of the 0–10 cm layer is lower after 53 years of cultivation than it is in nearby natural forests.¹⁹⁷ Cultivation also reduces soil aggregate stability,¹⁹⁸ exemplified by the fact that average bulk density of a rainforest soil is lower than in deforested areas.¹⁹⁹ These reductions in soil porosity lead to soil degradation due to changes in water infiltration and percolation.²⁰⁰

4.1.3 *Repairing Soil Degradation*

The challenge the world now faces is how to manage forests and agricultural lands proactively to deliver food and water to humans, while also preserving biodiversity and other ecosystem services.²⁰¹ Strategies to reduce or even reverse soil degradation include no-till farming, water conservation and harvest, cover cropping, woodland regeneration, agroforestry, improved grazing practices, more efficient irrigation and erosion control.^{181,179} Soil organic-matter content is of the utmost importance and can be improved by management practices that add biomass to the soil, reduce disturbance and improve soil structure.

4.1.4 *The Agroforestry Alternative*

From Conte,²⁰² “A forest understood as an agrarian landscape can include many centuries of forest-based husbandry.”^{203,204} For centuries, farmers in the eastern Arc Mountains of Africa used agroforestry in the mountains to cultivate native and introduced plants.^{205–209} At Mt. Kisagau, traditional botanical knowledge is tightly connected to a 1000 m elevation gradient and conveyed to generations through oral history that details the agro-ecological use of the entire mountain.²⁰² Farming once entailed a mosaic of forest ecosystems at varying stages of exploitation and regeneration that emphasised mobility, since water rather than temperature was a key factor of tree migration across Africa.²¹⁰ Farmers combined imported grain species with African beans, sorghum and millet,^{211,212} and there is evidence that Asian banana was possibly a feature in African agroforestry for more than 5000 years.²¹² More recently, western-style agricultural and forestry practices ignored lessons of indigenous land-use and forest evolution, emphasising timber yields only, and the landscape was quickly degraded to a point where indigenous trees could not even be replanted.²⁰² Agroforestry practices have been common for thousands of years in Europe, Africa and South America, and may hold the key to understanding how to use fertile forest soils to support all life without denuding and degrading them.

5 **Soil Characteristics as Tools for Adaptive Management**

Scientists are currently developing new tools based on soil characteristics to help farmers and land managers evaluate the potential effects of climate

change on soil water availability and develop appropriate strategies to adapt to the change or possibly mitigate negative climate impacts. Correlation models can incorporate the effects of geology, elevation and specific soil properties into a vulnerability index, estimating where crop or tree mortality will most probably occur during periods of prolonged drought or flood. With some awareness of this vulnerability, managers can implement practices to reduce soil erosion or decrease competition for scarce resources in areas at high risk of mortality, or they can focus soil quality restoration efforts in areas where forest or crop resilience is expected.

Soil physical characteristics are reliable predictors of forest health as the climate changes, because the temporal scale at which climate affects soil development is much longer (thousands to millions of years) than the scale at which climate is affecting trees (days, months or years). Soil characteristics constrain water and nutrient availability to forests and crops alike, and hold clues about how water might be moving through the soil. These factors can be indicators of whether rainfall is likely to evaporate or infiltrate, as well as the amount and duration of water storage in the rooting zone. Because they hold or release moisture based on their texture, depth and chemistry, soils can either mitigate or exacerbate climate change impacts to plants, affecting ecosystem vulnerability to heatwaves, wildfires and pest outbreaks. Therefore, soil characteristics hold the key for farmers and land managers seeking sustainable means to meet the food and energy demands of a growing population.

References

1. P. J. van Mantgem, N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fulé, M. E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor and T. T. Veblen, *Science*, 2009, **323**, 521–524.
2. C. D. Allen, A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J. -H. Lim, G. Allard, S. W. Running, A. Semerci and N. Cobb, *Forest Ecol. Manage.*, 2010, **259**, 660–684.
3. K. R. Samabaraju, A. L. Carroll, J. Zhu, K. Stahl, R. D. Morre and B. H. Aukema, *Ecography*, 2012, **35**, 211–223.
4. A. L. Westerling, H. G. Hidalgo, D. R. Cayan and T. W. Swetnam, *Science*, 2006, **313**, 940–943.
5. D. McKenzie, D. W. Peterson, D. L. Peterson and P. E. Thornton, *J. Biogeogr.*, 2003, **30**, 1093–1108.
6. P. Mote, A. M. Hamlet, M. P. Clark and D. P. Lettenmaier, *Am. Meteor. Soc.*, 2005, **86**, 1–39.
7. C. M. Brasier, *Ann. Sci. For.*, 1996, **53**, 347–358.
8. H. H. Rogers, J. F. Thomas and G. E. Bingham, *Science*, 1983, **220**, 428–429.
9. C. Rathgeber, A. Nicault, J. Guiot, T. Keller, F. Guibal and P. Roche, *Global Planetary Change*, 2000, **26**, 405–421.

10. M. A. Drummond and T. R. Loveland, *BioScience*, 2010, **60**, 286–298.
11. J. Steinkamp and W. Peterman, <http://app.databasin.org/app/pages/datasetPage.jsp?id=b2947eeae2e5488a86eacf0fcd4df7a4>, last accessed 10.05.2012.
12. W. R. Anderegg, J. A. Berry, D. D. Smith, J. S. Sperry, L. D. Anderegg and C. B. Field, *Proc. Natl. Acad. Sci. U. S. A.*, 2012, **109**, 233–237.
13. K. A. Cherkauer and D. P. Lettenmaier, *J. Geophys. Res.*, 1999, **104**, 19599–19610
14. Y. Iwata, M. Hayashi and T. Hirota, *Vadose Zone*, 2008, **7**, 79–86.
15. USGCRP, *Global Climate Impacts on the United States*, 2009; <http://www.globalchange.gov/publications/reports/scientific-assessments/us-impacts>, last accessed 10.05.2012.
16. S. Solomon, in *Climate Change 2007: The Physical Science Basis, Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, ed. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor and H. L. Miller, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2007.
17. S. Raper and R. J. Braithwaite, *Nature*, 2006, **439**, 311–313.
18. T. Kitzberger, T. W. Swetnam and T. T. Veblen, *Global Ecol. Biogeogr.*, 2001, **10**, 315–326.
19. Intergovernmental Panel on Climate Change (IPCC), *Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, 2007, Cambridge Univ. Press, Cambridge.
20. P. Ciais, M. Reichstein, N. Viovy, A. Granier, J. Ogée, V. Allard, M. Aubinet, N. Buchmann, C. Bernhofer, A. Carrara, F. Chevallier, N. De Noblet, A. D. Friend, P. Friedlingstein, T. Grünwald, B. Heinesch, P. Keronen, A. Knohl, G. Krinner, D. Loustau, G. Manca, G. Matteucci, F. Miglietta, J. M. Ourcival, D. Papale, K. Pilegaard, S. Rambal, G. Seufert, J. F. Soussana, M. J. Sanz, E. D. Schulze, T. Vesala and R. Valentini, *Nature*, 2005, **437**, 529–533.
21. FAO, *Forestry Paper 147, Global Forest Resource Assessment 2005, Main Report*, 2006, pp. 11–36.
22. H. Hoogeveen, *Climate Change*, 2007, **2**, 36–46.
23. J. E. Aukema, D.G. McCullough, B. Von Holle, A.M. Liebold, K. Britton and S. J. Frankel, *BioScience*, 2010, **60**, 886–897.
24. A. M. Liebold, W. L. M. MacDonald, D. Bergdahl and V. C. Mastro, *Forest Sci.*, 1995, **41**, 1–49.
25. D. S. Wilcove, D. Rothstein, J. Bubow, A. Phillips and E. Losos, *BioScience*, 1998, **48**, 607–615.
26. D. Simberloff, *Nature and Human Society*, National Academy Press, Washington DC, USA, 2000.
27. E. A. Allen and L. M. Humble, *Can. J. Plant Pathol.*, 2002, **24**, 103–110.
28. J. P. Shepard, M. J. Mitchell, T. J. Scott, Y. M. Zhang and D. J. Raynal, *Water, Air Soil Pollut.*, 1989, **48**, 225–238.

29. K. C. Weathers, M. L. Cadenasso and S. T. A. Pickett, *Conserv. Biol.*, 2001, **15**, 1506–1514.
30. C. T. Driscoll, *BioScience*, 2001, **51**, 180–198.
31. K. C. Weathers and A. Ponette-González, in *Forest Hydrology and Biogeochemistry: Synthesis of Past Research and Future Directions*, ed. D. F. Levia, D.E. Carlyle-Moses and T. Tanaka, Ecological Studies Series, No. 216, Springer-Verlag, Heidelberg, Germany, 2011.
32. R. A. Skeffington and E. Wilson, *Environ. Pollut.*, 1988, **54**, 159–184.
33. J. D. Aber, C. L. Goodale, S. V. Ollinger, M. L. Smith, A. H. Magill, M. E. Martin, R. A. Hallett and J. L. Stoddard, *BioScience*, 2003, **53**, 375–389.
34. S. E. Page, R. A. J. Wuest, D. Weiss, J. O. Riley, W. Shotyk and S. H. Limin, *J. Quat. Sci.*, 2004, **19**, 625–635.
35. J. Jaenicke, J. O. Riley, C. Mott, P. Kimman and F. Siegert, *Geoderma*, 2008, **147**, 151–158.
36. J. P. Andriess, *FAO UN Soils Bulletin*, 1988, **59**, 178.
37. R. A. Chimner and K. C. Ewel, *Wetlands Ecol. Manage.*, 2005, **13**, 671–684.
38. M. R. C. Posa, L. S. Wijedasa and R. T. Corlett, *BioScience*, 2011, **61**, 49–57.
39. A. Langner, J. Miettinen and F. Siegert, *Global Change Biol.*, 2007, **13**, 2329–2340.
40. A. Langner, F. Siegert, *Global Change Biol.*, 2009, **15**, 48–62.
41. M. R. Turetsky, W. F. Donahue and B. W. Benscoter, *Nature Commun.*, 2, 514.
42. S. E. Page, A. Hoscilo, A. Langner, K. Tansey, F. Siegert, S. Limin and J. Riley, in *Tropical Fire Ecology: Climate Change, Land Use and Ecosystem Dynamics*, ed. M. A. Cochrane, Springer-Praxis, Berlin, 2009, pp. 263–287.
43. U. Ballhorn, F. Siegert, M. Mason and S. Limin, *Proc. Natl. Acad. Sci. U. S. A.*, 2009, **106**, 21213–21218.
44. G. R. van der Werf, D. C. Morton, R. S. DeFries, J. G. J. Oliver, P. S. Kasibhatla, R. B. Jackson, G. J. Collatz and J. T. Randerson, *Nature Geosci.*, 2009, **2**, 737–739.
45. S. E. Page, F. Siegert, J. O. Rieley, H. -D. V. Boehm, A. Jaya and S. Limin, *Nature*, 2002, **420**, 61–65.
46. R. A. Betts, P. M. Cox, M. Collins, P. P. Harris, C. Huntingford and C. D. Jones, *Theor. Appl. Climatol.*, 2004, **78**, 157–175.
47. D. C. Nepstad, C. M. Stickler, B. S. Filho and F. Merry, *Philos. Trans. R. Soc. London, Ser. B*, 2008, **363**, 1737–1746.
48. B. S. Soares-Filho, D. C. Nepstad, L. M. Curran, G. C. Cerqueira, R. A. Garcia, C. A. Ramos, E. Voll, A. McDonald, P. LeFebvre and P. Schlesinger, *Nature*, 2006, **440**, 520–523.
49. J. G. Canadell, C. Le Quéré, M. R. Raupach, C. B. Field, E. T. Buitenhuis, P. Ciais, T. J. Conway, N. P. Gillett, R. A. Houghton and G. Marland, *Proc. Natl. Acad. Sci. U. S. A.*, 2007, **104**, 18866–18870.
50. C. A. Nobre, P. J. Sellers and J. Shukla, *J. Climate*, 1991, **4**, 957–988.

51. P. M. Cox, R. A. Betts, C. D. Jones, S. A. Spall and I. J. Totterdell, *Nature*, 2000, **408**, 184–187.
52. P. M. Cox, R. A. Betts, M. Collins, P. P. Harris, C. Huntingford and C. D. Jones, *Theor. Appl. Climatol.*, 2004, **78**, 137–156.
53. A. Botta and J. A. Foley, *Global Biogeochem. Cycles*, 2002, **16**, 1070.
54. M. D. Oyama and C. A. Nobre, *Geophys Res Lett.*, 2003, **30**, 2199.
55. Y. Malhi, L. E. O. C. Aragão, D. Galbraith, C. Huntingford, R. Fisher, P. Zelazowski, S. Sitch, C. McSweeney and P. Meir, *Proc. Natl. Acad. Sci. U. S. A.*, 2009, **106**, 20610–20615.
56. R. Betts, M. Sanderson and S. Woodward, *Philos. Trans. R. Soc. London, Ser. B*, 2008, **363**, 1873–1880.
57. D. C. Nepstad, C. M. Stickler, B. S. Soares-Filho and F. Merry, *Philos. Trans. R. Soc. London, Ser. B*, 2008, **363**, 1737–1746.
58. S. Woodward, D. Roberts and R. Betts, *Geophys. Res. Lett.*, 2005, **32**, L18810.
59. J. Lean and P. R. Rowntree, *J. Climate*, 1997, **10**, 1216–1235.
60. D. C. Nepstad, C. R. De Carvalho, E. A. Davidson, P. H. Jipp, P. A. Le Feuvre, G. H. Negreiros, E. S. Da Silva, T. A. Stone, S. E. Trumbore and S. Vieira, *Nature*, 1994, **372**, 666–669.
61. D. C. Nepstad, P. Lefebvre, U. Lopes da Silva, J. Tomasella, P. Schlesinger, L. Solórzano, P. Moutinho, D. Ray and J. Guerreira Benito, *Global Change Biol.*, 2004, **10**, 704–717.
62. D. C. Nepstad, I. M. Tohver, D. Ray, P. Moutinho and G. Cardinot, *Ecology*, 2007, **88**, 2259–2269.
63. M. G. Hodnett, L. Pimental da Silva, H. R. da Rocha and R. Cruz Senna, *J. Hydrol.*, 1995, **170**, 233–254.
64. R. S. Oliveira, R. E. Dawson, S. S. O. Burgess and D. C. Nepstad, *Oecologia*, 2005, **145**, 354–363.
65. P. M. Brando, D. C. Nepstad, E. A. Davidson, S. E. Trumbore, D. Ray and P. Camargo, *Philos. Trans. R. Soc. London, Ser. B*, 2008, **363**, 1839–1848.
66. G. B. Williamson, W. F. Laurence, A. A. Oliveira, P. Delamônica, G. Gascon, T. E. Lovejoy and L. Pohl, *Conserv. Biol.*, 2000, **14**, 1538–1542.
67. D. Ray, D. C. Nepstad and P. Montinho, *Ecol. Appl.*, 2005, **15**, 1664–1678.
68. L. R. Iverson and A. M. Prasad, *Ecosystems*, 2001, **4**, 186–199.
69. USDA, Forest Inventory Analysis, 2009; <http://fia.fs.fed.us/library/bus-org-documents/>, last accessed 10.05.2012.
70. N. Coops, R. H. Waring and B. E. Law, *Ecol. Modelling*, 2005, **183**, 107–124.
71. N. Coops and R. H. Waring, *Climate Change*, 2010, **105**, 313–328.
72. N. Coops, R. H. Waring, C. Beier, R. R. Jauvin and T. Wang, *Appl. Vegetat. Sci.*, 2011, **14**, 402–414.
73. A. Fajardo, E. J. B. McIntire, *J. Ecol.*, 2012.
74. J. Lenoir, J. C. Gégout, P. A. Marquet, P. de Ruffray and H. Brise, *Science*, 2008, **320**, 1768–1771.
75. F. Archaux, *Ibis*, 2004, **146**, 138.
76. S. Popy, L. Bordignon and R. Prodon, *J. Biogeogr.*, 2010, **37**, 57.

77. S. M. Crimmins, S. Z. Dobrowski, J. A. Greenberg, J. T. Abatzoglou and A. R. Mynsberge, *Science*, 2011, **331**, 324–327.
78. C. I. Millar, L. J. Graumlich, D. L. Delany, R. D. Westfall and J. K. King, *Arct. Alp. Res.*, 2004, **36**, 181.
79. A. J. Eckert and M. L. Eckert, *Madrono*, 2007, **54**, 117.
80. A. Kattenberg A. F. Giorgi, H. Grassl, G. A. Meehl, J. F. B. Mitchell, R.J. Stouffer, T. Tokioka, A. J. Weaver and T. M. L. Wigley, in *The Science of Climate Change: Contribution of Working Group I to the Second Assessment of the IPCC*, 1996, Cambridge University Press, UK, pp. 285–357.
81. M. C. Serreze, J. E. Walsh, F. S. Chapin, T. Osterkamp, M. Dyurgerov, V. Romanovsky, W. C. Oechel, J. Morison, T. Zhang and R. G. Barry, *Climate Change.*, 2000, **46**, 159–207.
82. L. A. Viercek and C. T. Dyrness, in *Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function*, ed. K. Van Cleve, F. S. Chapin, III, P. W. Flanagan, L. A. Vierick and C. T. Dyrness, Springer-Verlag, New York, 1986, pp. 22–43.
83. C. Potter, *Ecol. Modelling*, 2004, **175**, 1–24.
84. R. V. Densmore, *Am. J. Bot.*, 1997, **84**, 274–278.
85. D. V. D'Amore and P. E. Hennon, *Global Change Biol.*, 2006, **12**, 524–545.
86. P. E. Hennon, C. G. Shaw III and E. M. Hansen, *Plant Disease*, 1990, **74**, 267–273.
87. C. G. Shaw III, A. Eglitis, T. H. Laurent and P. E. Hennon, *Plant Disease*, 1985, **69**, 13–17.
88. P. E. Hennon, G. B. Newcomb, C. G. Shaw III and E. M. Hansen, *Plant Disease*, 1986, **70**, 352.
89. E. M. Hansen, P. B. Hamm, C. G. Shaw III and P. E. Hennon, *Trans. Br. Mycolog. Soc.*, 1988, **91**, 379–384.
90. P. B. Hamm, E. M. Hansen, P. E. Hennon and C. G. Shaw III, *Trans. Br. Mycolog. Soc.*, 1988, **91**, 385–388.
91. P. E. Hennon, *Mycologia*, 1990, **82**, 59–66.
92. P. E. Hennon, E. M. Hansen and C. G. Shaw III, *Northwest Sci.*, 1990, **64**, 45–54.
93. P. E. Hennon and M. J. McWilliams, *Can. J. Forest Res.*, 1999, **29**, 1985–1988.
94. J. A. Antos and D. B. Zobel, *Can. J. Bot.*, 1986, **64**, 1898–1909.
95. W. L. Chapman and J. E. Walsh, *Bull. Am. Meteorol. Soc.*, 1993, **74**, 33–47.
96. R. J. Hebda, *Geogr. Phys. Quat.*, 1995, **49**, 55–79.
97. FAO, *State of the World's Forests*, Rome, 2011; <http://www.fao.org/docrep/013/i2000e/i2000e00.htm>, last accessed 10.05.2012.
98. J. A. Jones, G. L. Achterman, L. A. Augustine, I. F. Creed, P. F. Folliott, L. MacDonald and B. C. Wemple, *Hydrol Process*, 2009, **23**, 2699–2704.
99. USGCRP; <http://www.globalchange.gov/component/content/article/52-reports-and-assessments/345-looking-at-americas-climate>, last accessed 05.04.2012.
100. J. Tang and Q. Zhuang, *Climatic Change*, 2011, **107**, 481–510.

101. J. S. Kimball, K. C. McDonald and M. Zhao, *Earth Interact.*, 2006, **10**, 1–22.
102. G. A. Meehl and T. F. Stocker, in *Climate Change 2007: the Physical Science Basis*, ed. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor and H. L. Miller, Cambridge University Press, Cambridge, 2007.
103. G. Saramiento, in *High Altitude Tropical Biogeography*, ed. F. Vuilleumier and M. Monasterio, Oxford University Press, Oxford, 1986, pp. 11–45.
104. K. S. H. Peh, M. C. K. Soh, N. S. Sodhi, W. F. Laurence, D. J. Ong and R. Clements, *BioScience*, 2011, **61**, 27–38.
105. H. J. Boehmer, in *Coping with Global Environmental Change, Distasters and Security*, ed. H. G. Brauch, U. O. Spring, C. Mesjasz, J. Grin, P. Kameri-Mbote, B. Chourou, P. Dunay and J. Birkman, Springer-Verlag, Berlin-Heidelberg-New York, 2011, p. 790–802.
106. N. S. Sodhi and B. W. Brook, *Southeast Asia Biodiversity in Crisis*, Cambridge University Press, Cambridge, UK, 2006.
107. L. Ong, MSc thesis, National University of Singapore, 2000.
108. P. Bubb, I. May, L. Miles and J. Sayer, *Cloud Forest Agenda*, UN Environment Programme World Conservation Monitoring Centre, 2004.
109. T. K. Waggener, in *Asia-Pacific Forestry Sector Outlook Study – Working Paper Series*, FAO, 1997.
110. C. Doumenge D. Gilmour, M. R. Perez and J. Blockhus, in *Tropical Montane Cloud Forests*, ed. L. S. Hamilton, J. S. Juvik and F. N. Scatena, 1995, pp. 24–37.
111. K. W. Leong and N. W. Chan, in *Cameron Highlands*, ed. N. W. Chan, 2006, pp. 121–132.
112. L. A. Bruijnzeel and E. J. Veneklaas, *Ecology*, 1998, **79**, 3–9.
113. USGCRP, *Global Climate Impacts on the United States*, 2009; <http://www.globalchange.gov/publications/reports/scientific-assessments/us-impacts>, last accessed 10.05.2012.
114. T. Hudiburg, B. Law, D. P. Turner, J. Campbell, J. Donato and M. Duane, *Ecol. Appl.*, 2009, **19**, 163–180.
115. K. Lajtha and F. J. Barnes, *Tree Physiol.*, 1991, **9**, 59–67.
116. C. Potter, *Ecol. Modelling*, 2004, **175**, 1–24.
117. G. P. Asner and S. Archer, in *Livestock in a Changing Landscape: Drivers, Consequences and Responses*, ed. H. Steinfeld, H. Mooney, F. Schneider, L. E. Neville, Washington, DC, Island Press, 2010, pp. 69–82.
118. K. A. Hibbard, S. Archer, D. S. Schimel and D. W. Valentine, *Ecology*, 2001, **82**, 1999–2011.
119. R. F. Hughes, G.P. Asner, C. A. Wessman, C. McMurtry, J. Nelson and R. J. Ansley, *Global Change Biol.*, 2006, **12**, 1733–1747.
120. A. K. Knapp, J. M. Briggs, S. L. Collins, S. R. Archer, M. S. Bret-Harte, B. E. Ewers, D. P. Peters, D. R. Young, G. R. Shaver, E. Pendall and M. B. Cleary, *Global Change Biol.*, 2008, **14**, 615–623.

121. N. N. Barger, S. R. Archer, J. L. Campbell, C. H. Huang, J. Morton and A. K. Knapp, *J. Geophys. Res.*, 2011, **116**, 1–17.
122. W. H. Schlesinger, *Biogeochemistry: An Analysis of Global Change*, Academic Press, New York, 2nd edn, 1997.
123. T. B. Bragg and L. C. Hulbert, *J. Range Manage.*, 1976, **29**, 19–24.
124. S. Archer, C. J. Scifres, C. Bassham and R. Maggio, *Ecol. Monogr.*, 1988, **58**, 111–127.
125. D. R. Lane, D. P. Coffin and W. K. Lauenroth, *J. Veg. Sci.*, 1998, **9**, 239–250.
126. R. J. Ansley and M. J. Castellano, *Restorat. Ecol.*, 2006, **14**, 420–428.
127. J. M. Briggs, G. A. Hoch and L. C. Johnson, *Ecosystems*, 2002, **5**, 578.
128. S. C. Goslee, K. M. Harstad, D. P. C. Peters, A. Rango and W. H. Schlesinger, *Arid Environ.*, 2003, **54**, 755–767.
129. R. B. Jackson, H. J. Schenk, E. G. Jobbágy, J. Canadell, G. D. Colello, R. E. Dickinson, C. B. Field, P. Friedlingstein, M. Heimann, K. Hibbard, D. W. Kicklighter, A. Kleidon, R. P. Neilson, W. J. Parton, O. E. Sala and M. T. Sykes, *Ecol. Appl.*, 2000, **10**, 470–483.
130. R. B. Jackson, J. L. Banner, E. G. Jobbágy, W. T. Pockman and D. H. Wall, *Nature*, 2002, **418**, 623–626.
131. C. A. Wessman, S. Archer, L. C. Johnson and G. P. Asner, in *Land Change Science: Observing, Monitoring and Understanding Trajectories of Change on the Earth*, ed. G. Gutman, A. C. Janetos, C.O. Justice, E. F. Moran, J. F. Mustard, R. R. Rindfuss, D. Skole, B. L. Turner II and M. A. Cochrane, Kluwer Acad., Dordrecht, Netherlands, 2004, pp. 185–208.
132. S. Archer, in *Ecological Implications of Livestock Herbivory in the West*, ed. M. Vavra, W. A. Laycock and R. D. Pieper, Society for Range Management, Denver, CO, 1994, pp. 13–68.
133. S. Archer, D. S. Schimel and E. A. Holland, *Climate Change*, 1995, **29**, 91–99.
134. O. W. Van Auken, *Annu. Rev. Ecol. Syst.*, 2000, **31**, 197–215.
135. E. G. Jobbágy and R. B. Jackson, *Ecol. Appl.*, 2000, **10**, 423–436.
136. T. W. Boutton, J. D. Liao, T. R. Filley, S. R. Archer and R. Follett, in *Soil Carbon Sequestration and the Greenhouse Effect*, ed. R. Lal and R. Follett, 2008, pp. 181–205.
137. Y. Bai, T. Colberg, J. T. Romo, B. McConkey, D. Pennock and R. Farrell, *Agric. Ecosyst. Environ.*, 2009, **134**, 269–276.
138. J. Canadell, R. B. Jackson, J. R. Ehleringer, H. A. Mooney, O. E. Sala and E. D. Schulze, *Oecologia*, 1996, **108**, 583–595.
139. R. B. Jackson, J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala and E. D. Schulze, *Oecologia*, 1996, **108**, 389–411.
140. T. W. Boutton, S. R. Archer, A. J. Midwood, S. F. Zitzer and R. Bol, *Geoderma*, 1998, **82**, 5–41.
141. L. A. Biderman and T. W. Boutton, *Soil Biol. Biochem.*, 2009, **41**, 1943–1950.
142. A. J. Franzluebbers and M. A. Arshad, *Can. J. Soil Sci.*, 1996, **76**, 387–393.
143. A. J. Franzluebbers and M. A. Arshad, *Soil Sci. Soc. Am. J.*, 1997, **61**, 1382–1386.

144. R. A. Gill and I. C. Burke, *Oecologia*, 1999, **121**, 551–563.
145. J. D. Liao, T. W. Boutton and J. D. Jastrow, *Soil Biol. Biochem.*, 2006, **38**, 3184–3196.
146. C. J. Field, J. Merino and H. A. Mooney, *Oecologia*, 1983, **60**, 384–389.
147. K. Lajtha and W. G. Whitford, *Oecologia*, 1989, **80**, 341–348.
148. H. G. Miller and J. D. Miller, *J. Appl. Ecol.*, 1976, 249–256.
149. H. Brix, *Can. J. For. Res.*, 1981, **11**, 502–511.
150. M. R. Keyes, C. C. Grier, *Can. J. For. Res.*, 1981, **11**, 599–605.
151. S. Linder and D. A. Rook, in *Nutrition of Plantation Forests*, ed. G. D. Bowen, E. K. S. Nambiar, Academic Press, London, 1984, pp. 211–263.
152. K. J. Nadelhoffer, J. D. Aber and J. M. Melillo, *Ecology*, 1985, **66**, 1377–1390.
153. S. Linder, in *Potentials and Limitations of Ecosystem Analysis*, ed. E. D. Schulze and H. Z. Wolfer, Springer-Verlag, Berlin, 1987, pp. 180–202.
154. B. J. Myers, *Tree Physiol.*, 1988, **4**, 315–323.
155. D. Sanantonio, in *Biomass Production by Fast-Growing Trees*, ed. J. S. Pereira and J. J. Landsberg, Kluwer Academic Publishers, The Netherlands, 1989, pp. 57–72.
156. R. J. Raison and R. Stottlemeyer, *Tree Physiology*, 1991, **9**, 209–225.
157. J. L. Charley in *Wildland Shrubs – Their Biology and Utilization*, ed. C. M. McKell, J. P. Blaisdell and J. R. Goodwin, Intermountain Forest and Range Research Station, US Department of Agriculture, Ogden, Utah, 1972, pp. 182–203.
158. J. A. Ludwig in *Larrea Derie el Desierto*, ed. E. C. Lopez, T. J. Mabry and S. F. Tavizopp, Centro de Investigacion en Quimica Aplicada, Saltillo, Coahila, Mexico, 1979, pp. 139–150.
159. J. F. Reynolds and G. L. Cunningham, *Oecologia*, 1981, **51**, 357–363.
160. A. Ayanaba, S. B. Tuckwell and D. S. Jenkinson, *Soil Biol. Biochem.*, 1976, **8**, 519–525.
161. J. M. Shurer, *Soil Biol. Biochem.*, 1985, **17**, 611–618.
162. D. S. Powlson and P. C. Prookes, *Soil Biol. Biochem.*, 1987, **19**, 159–164.
163. S. Perakis and E. R. Sinkhorn, *Ecology*, 2011, **92**, 1481–1491.
164. L. M. Christensen, G. M. Lovett, K. Weathers and M. Arthur, *Soil Sci. Soc. Am. J.*, 2009, **73**, 638–646.
165. P. N. Beets and H. A. I. Madgwick, *N. Z. J. For. Sci.*, 1988, **18**, 43–64.
166. S. K. Chapman, J. A. Langley, S. C. Hart and G. W. Koch, *New Phytologist*, 2006, **169**, 27–34.
167. G. E. Likens, F. H. Bormann, R. S. Pierce, J. S. Eaton and N. M. Johnson, *Biogeochemistry of a Forested Ecosystem*, Springer-Verlag, New York-Heidelberg-Berlin, 1977, p. 146.
168. P. M. Vitousek and J. M. Melillo, *For. Sci.*, 1979, **25**, 605–619.
169. P. M. Vitousek, *Ecology*, 1984, **66**, 1360–1376.
170. R. J. Raison, P. K. Khanna and P. V. Woods, *Can. J. For. Res.*, 1985, **15**, 657–664.
171. A. M. O’Connell, *For. Ecol. Manage.*, 1989, **26**, 95–111.

172. R. J. Raison, P. K. Khanna and P. V. Woods, *Can. J. For. Res.*, 1985, **15**, 132–140.
173. N. W. Foster, J. A. Nicolson and P. W. Hazlett, *J. Environ. Qual.*, 1989, **18**, 238–244.
174. R. Stottlemeyer and D. Rutkowski. *Water Resour. Res.*, 1990, **26**, 721–737.
175. R. Lea, W. C. Tierson, D. H. Bickelhaupt and A. L. Leaf, *Plant Soil*, 1980, **54**, 419–439.
176. H. L. Mitchell, *Black Forest Bull.*, 1939, 11.
177. C. M. Rascher, C. T. Driscoll and N. E. Peters, *Biogeochemistry*, 1987, **3**, 209–224.
178. S. Bernal, L. O. Hedin, G. E. Likens, S. Gerber and D. C. Buso, *Proc. Natl. Acad. Sci. U. S. A.*, 2012, **109**, 3406–3411.
179. J. Kaiser, *Science*, 2004, **304**, p. 1616.
180. J. L. Smith, J. J. Halvorson and R. I. Papendick, *Soil Sci. Am. J.*, 1994, **57**, 743–749.
181. L. R. Oldeman, in *ISRIC Bi-Annual Report*, Netherlands, 1992, pp. 19–36.
182. R. Lal, *Science*, 2004, **304**, 1623.
183. J. Gaillardet, B. Dupre, P. Louvat and C. J. Allegre, *Chem. Geol.*, 1999, **159**, 3–30.
184. P. A. Raymond and J. J. Cole, *Science*, 2003, **301**, 88–91.
185. G. Bayon, B. Dannielou, J. Etoubleau, E. Ponzevera, S. Toucanne and S. Bernell, *Science*, 2012, **335**, 1219–1222.
186. T. N. Huffman, *Annu. Rev. Anthropol.*, 1982, **11**, 133.
187. J. Vansina, *J. Afr. Hist.*, 1984, **25**, 129.
188. D. W. Phillipson, *African Archaeology*, Cambridge University Press, Cambridge, 1993.
189. C. J. Holden, *Proc. R. Soc. London, Ser. B*, 2002, **269**, 793.
190. J. Diamond and P. Bellwood, *Science*, 2003, **300**, 597.
191. K. J. Willis, L. Gillson and T. M. Brncic, *Science*, 2004, **304**, 402.
192. A. Vincens, D. Schwartz, H. Elenga, I. Reynaud-Farrera, A. Alexandre, J. Bertaux, A. Mariotti, L. Martin, J. -D. Meunier, F. Nguetsop, M. Servant, S. Servant-Vildary and D. Wirmann, *J. Biogeogr.*, 1999, **26**, 879.
193. J. A. Maley, *Inst. Dev. Studies Bull.*, 2002, **33**, 13.
194. F. J. Stevenson, *Cycles of Soil: Carbon, Nitrogen, Phosphorus, Sulfur, Micronutrients*, John Wiley and Sons, New York, 1999.
195. F. Khormali, M. Ajami, S. Ayoubi, Ch. Srinivasarao and S. P. Wani, *Agric. Ecosyst. Environ.*, 2009, **134**, 178–189.
196. T. G. Vagen, *Geoderma*, 2006, **131**, 190–200.
197. M. Lemenih and D. Teketay, *Agric. Ecosyst. Environ.*, 2005, **105**, 373–386.
198. J. Six, K. Paustian, E. T. Elliott and C. Combrink, *Soil Sci. Soc. Am. J.*, 2000, **64**, 681–689.
199. V. Rasiah, S. K. Florentine, B. L. Williams and M. E. Westbrooke, *Geoderma*, 2004, **120**, 35–45.
200. K. Zhang, S. Li, W. Peng and B. Yu, *Soil Till Res.*, 2004, **76**, 157–165.
201. R. B. Jackson and J. S. Baker, *BioScience*, 2010, 2010, **60**, 698–707.

202. C. Conte, *BioScience*, 2010, **60**, 309–313.
203. L. Rival, in *Advances in Historical Ecology*, ed. W. Balee, Columbia University Press, New York, 1998, pp. 232–250.
204. E. Krieke, in *History and African Environments*, ed. W. Beinert and J. McGregor, Currey, Oxford, 2003, pp. 27–42.
205. S. Feierman, *The Shambaa Kingdom*, University of Wisconsin Press, Madison, 1974.
206. J. E. G. Sutton, *Azania*, 1989, **24**, 98–112.
207. P. Schmidt, in *Historical Ecology Cultural Knowledge and Changing Landscape*, ed. C. Crumley, School of American Research Press, Santa Fe, 1994, pp. 232–250.
208. J. Vansina, *J. Afr. Hist.*, 1995, **36**, 173–195.
209. C. Ehret, *An African Classical Age: Eastern and Southern Africa in World History, 1000 BC to AD 400*, University of Virginia, Charlottesville, 2001.
210. A. C. Hamilton, *Environmental History of East Africa: A Study of the Quaternary*, Academic Press, New York, 1982.
211. O. Warburg, *Die Kulturpflanzen Usambaras, Mitteilungen aus den Deutschen Schutzgebieten*, 7, 1894, pp. 131–199.
212. B. J. Lejju, P. Robertshaw and D. Taylor, *J. Arch. Sci.*, 2006, **33**, 102–113.