Chapter 10:

Impacts of natural disturbance on soil carbon dynamics in forest ecosystems.

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INTRODUCTION

Forest soils are entities within themselves, self-organized and highly resilient over time. The transfer of energy bound in carbon (C) molecules drives the organization and functions of this biological system (Fisher and Binkley, 2000; Paul and Clark, 1996). Photosynthetic organisms reduce atmospheric C and store energy from solar radiation in the formation of complex C molecules. This bound energy is transferred to mineral soil in the form of litterfall, root turnover, and root exudates supporting an intricate detrital trophic structure (Fisher, 1995). Much of the C moving through this detrital food web is released annually back to the atmosphere as CO_2 from respiration (see Chapter 7), but resident in the mineral soil is a large pool of C that is recalcitrant to decomposition.

Interest in the ability of forest soils to store atmospheric C derived from anthropogenic sources has grown in recent years (Johnson, 1992; Heath and Smith, 2000; Cardon et al., 2001; Johnson and Curtis, 2001). Prior to the 1920s, deforestation was the primary source of increasing atmospheric C, but has since been surpassed by fossil fuel combustion (Vitousek, 1991). Reduced harvests on National Forest lands and reforestation on abandoned agricultural lands since the 1950s have increased some terrestrial C pools in the United States (Houghton et. al. 1999), yet this increase may be at risk due to altered temporal and spatial scales of disturbances (Murray et al., 2000). The extent to which these altered disturbance events have already affected many of the forests within the United States is considerable (see Chapter 2). This paper examines the importance of natural disturbance in shaping forest landscapes and the relationship between aboveground impacts and mineral soil carbon dynamics.

HISTORICAL PERSPECTIVE OF DISTURBANCE IN FORESTS

Disturbance has been defined as destructive events and environmental fluctuations that cause change in conditions of an ecological system (White and Pickett, 1985; Kaufmann et al., 1994). Traditionally, disturbances caused by fire, insects, disease, drought, and wind, were considered destructive; however, more recently these events have come to be regarded as key to ecological processes in forest function and are important in succession of forest ecosystems.

Clements (1916, 1928) defined succession as the progressive occupation of an area by different species associations from an initial pioneer community to a mature, stable "climax" community driven by regional climate. Succession was further classified as either primary or secondary. Primary succession occurred on newly formed or exposed substrates with no biological legacy. Secondary succession differed in that disturbance temporarily impeded development of the existing community, but progression toward a "climax" community resumed due to inherited biological factors, such as a developed soil with viable biological propagules.

In Clements' model, climate was the determining factor and the community a reflection of that climate. Substrates were of minor importance in the replacement of higher life forms as the community moved toward a stable climax stage. Disturbance only interrupted this progressive development toward equilibrium with the regional climate. Further additions to the Clementsian model proposed concepts of increasing species diversity and complexity, greater biomass, and floristic stability as attributes of communities moving along this directional pathway (Odum, 1969; Whittaker, 1975).

The effects of disturbance regimes in structuring forest communities took on greater significance with further study of succession in terrestrial ecosystems (Pickett, 1980; White, 1978). Pickett (1980) considered competitive exclusion as the driving mechanism moving succession toward an equilibrium community; however White (1978) noted that forest stands seldom reached the competitive exclusion stage, becoming increasingly susceptible to disturbance with age. What ecological community reoccupies a site following disturbance is often determined by the severity and frequency of the disturbance (Oliver 1981; Pickett 1980), with potential for establishment of alternate communities (Connell and Slatyer, 1977). This concept of non-equilibrium succession had its beginning in earlier works of Watt (1947) and Raup (1957).

Hollings (1973) furthered this concept of non-equilibrium succession and introduced the idea of resilience. Resilience is defined as the minimum disturbance necessary to disrupt a system and cause it to move to a new equilibrium state. Hollings (1980) considered natural disturbances integral to the normal functioning of ecosystems.

Prior to Hollings (1973) conceptual model, the major functions controlling community succession were thought to be exploitation and conservation. Exploitation focused on the rapid colonization of a newly disturbed area while conservation was the accumulation and storage of energy and material over time. Hollings (1995) added two additional concepts to this model, release and reorganization. As biomass and nutrients accumulate within an ecosystem, disturbance agents such as fire and insects can rapidly release this accumulation. Accumulation of material and energy becomes more susceptible to disturbance over time as it becomes more tightly bound within the system. Reorganization is the ability of soil processes to mobilize and immobilize nutrients, minimizing loss and making them available for the next phase of exploitation (Hollings, 1995).

DISTURBANCE EFFECTS ON FOREST SOIL CARBON

Soil C is the largest terrestrial C pool in forest ecosystems (Cardon et al., 2001). Accurate assessment of how this pool is altered following disturbance is crucial for determining the capacity of forest ecosystems to store C. Soil organic matter inputs come primarily from plant residues and root exudates (Paul and Clark, 1996; Senesi and Loffredo, 1998). Plant residue inputs from aboveground primary production contributes significant quantities of organic matter to soil, yet annual fine root production coupled with relatively slow decomposition rates has been shown to be of similar magnitude (McClaugherty et al., 1982). Decomposition of detrital organic matter by heterotrophic soil organisms returns C in the form of CO_2 back into the atmosphere through respiration, but also transforms a portion of this material into humic substances that are resistant to further chemical and microbial degradation (see Chapters 6, 7).

Conservation of SOM is a function of stability and turnover of the different C pools (Swift, 2001). The time required to attain a new steady-state of soil organic C is dependent on severity and duration of the disturbance, residual C pools that remain, organic matter inputs from the new vegetative community, and interaction of climate and time since last disturbance event. In post-disturbance reorganization, the readily decomposable C pool may be depleted in the surface layer, while resistant C is conserved. This resistant C pool can be up to half the total C in soil (Buyanovsky et al., 1994, Swift, 2001).

The change in total soil C is the summation of easily decomposable, moderately decomposable, and resistant C pools (Figure 1). Classification of soil C pools is based on differences in decomposability, with the understanding that there is considerable heterogeneity within each classification (see Chapter 9). Depending on the severity and type of disturbance, the degree to which different C pools in the mineral soil are impacted can bring about new steady-states in total soil C. Changes to the readily decomposable C pool in the surface mineral horizons resulting from disturbance may be large while resistant C is unaffected. Altered forest floor inputs also exert considerable control on rate of SOM accumulation depending on decomposability (i.e. woody material vs. leaves). The extent of change in different soil C pools following disturbance over large spatial scales has not been investigated.

FIRE

Fire impacts the physical, chemical, and biological resources of an ecosystem (DeBano et al., 1998; Neary et al., 2000). These effects vary with intensity and duration of fires along a

severity continuum that is controlled at both the regional (climate) and local scale (topography). Climate and topography also control frequency, size, and season of natural fires (Hyerdahl et al., 2001).

Fire is defined as a rapid, persistent exothermic chemical reaction that releases energy from the combination of combustible substances and oxygen. Fire in forest ecosystems is the transfer of chemical energy bound in live and dead trees, herbaceous understory, coarse woody debris, forest floor, and organic matter in the mineral soil to the surrounding environment in the form of heat through several physical processes. These processes include radiation, conduction, convection, mass transport, vaporization, and condensation (Pyne et al., 1996; DeBano et al. 1998).

Lightning is the principal ignition source for non-anthropogenic caused forest fires. The core of a lightning channel, between 6,000 and 12,000 K, exposes woody fuels to extreme temperatures for the duration of the flash (Pyne et al., 1996). Once ignited, thermal radiation or convection from the advancing fire front drives water from the surface of a fuel, elevates fuel temperatures, and then decomposes organic matter by pyrolysis, followed by combustion (DeBano et al., 1998).

Heat of combustion is transmitted in all directions with approximately 10 to 15 percent being transferred downward into mineral soil (Raison et al., 1986). The degree of change in soil organic matter (SOM) is dependent on duration and magnitude of the heat pulse (Hungerford, 1990; DeBano et al., 1998). This downward movement of heat initially increases soil temperatures to levels that thermally decompose organic matter. If the heat pulse is maintained longer or temperature increases further, then combustion of SOM can occur.

Soil heating during fire in forest ecosystems varies widely between low-severity surface fires to high-severity crown fires. Several variables affect severity such as wind speed and direction, fuel conditions, and microrelief (Raison, 1979). Microrelief is an important factor on soil and fuel moisture, but also influences spatial distribution and type of fuels available for combustion (Heyerdahl et al., 2001). Low-severity fires combust only surface fuels and transfer little heat downward, while high-severity fires can transfer considerable heat to the mineral soil over a sustained period of time (Table 1).

Within the United States, fire and insect suppression have affected disturbance regimes so greatly that the state of forest ecosystems is outside their range of natural variability. An example of this expanded scale is wildfire in the Interior West forest ecosystems. Fire suppression over the last half of the 20th century has resulted in considerable biomass accumulations in forests of this area making them fragile and susceptible to catastrophic fire (Covington and Moore, 1994; Neary et al., 1999) but with lower frequency of events (Swetnam, 1990). Fire suppression has also decreased the size of events, extending the range of variability of small spatial-scale occurrences. The decrease in small-scale fires allows greater accumulation of fuels over longer time periods. Fire severity is dependent on several physical factors discussed earlier, but just as important is time since the last disturbance.

The cessation of frequent, small-to-moderate fires potentially increases the severity when the next disturbance event occurs. Tillman et al. (2000) showed significant accumulation of C in tree biomass and coarse roots as the result of fire suppression in a Minnesota oak savanna compared to moderate and high frequency fire events. Houghton et al. (1999) also report increased C accumulation from “thickening” of western coniferous forests due to fire suppression. With increased forest floor accumulations (Sackett et al., 1996) and stand density (Neary et al., 1999) the likelihood of a high-severity wildfire is amplified (see Chapter 13).

Fire is typically thought of as a source of CO_2 released into the atmosphere, but the process also sequesters some C when organic matter is incompletely oxidized leaving charcoal at the soil surface (Johnson, 1992; Swift, 2001). This material is extremely resistant to decomposition, with mean residence times on the scale of 10,000 years (Swift, 2001). Charcoal inputs to the soil in fire-prone forest ecosystems can be considerable over long time periods, but to what extent is unknown (Johnson, 1992; Johnson and Curtis, 2001).

In a meta-analysis of fire effects on soil C and N, Johnson and Curtis (2001) found no significant effect on total C in either the A horizon or the whole soil. Their analysis included both

prescribed and wildfire from 13 studies across eight forest types, one woodland type, and a chaparral ecosystem. A significant increase in soil C did occur after ten or more years at one site, which they attributed to the increase in N-fixing microorganisms following fire (Johnson, 1992; 2001). For time periods shorter than 10 years, they found that prescribed fires had lower soil C while wildfires had generally higher soil C compared to the controls. If the premise that prescribed fire is of lower severity than wildfire is valid, then this result appears counterintuitive. However, they attributed this increase in mineral soil C to deposition of charcoal and hydrophobic organic compounds transferred from the forest floor to the mineral soil.

Physical Soil Properties

Destruction of SOM by fire can affect physical properties essential for maintaining soil structure. Loss of soil structure reduces bulk density and porosity of the soil, decreases infiltration, and increases runoff and erosion (DeBano et al., 1998; Neary et al., 2000). The extent of soil structural degradation due to organic matter combustion depends on magnitude and duration of soil heating (Debano et al., 1998; Wells et al., 1979).

Soil structure results from the complex interactions between organic C molecules, soil organisms, and mineral soil particles. Soil stability, bulk density, and porosity are structural properties that make available water, air, and nutrients to plant roots (Paul and Clark, 1996; Van Cleve and Powers, 1995). Structural integrity deteriorates as organic matter begins to decompose at 200^{o}C, with complete destruction at 500^{o}C (DeBano et al., 1998).

Organic matter aggregation of mineral soil particles improves water retention as well as structure (DeBano et al., 1998). Soil organic matter loss following fire can adversely affect hydrologic properties of the soil. The volume and rate of air and water movement through soil is controlled by pore size and space. When surface temperatures exceed 250^{o}C (Table 1) enough heat is transferred downward into surface soil horizons to initiate thermal destruction of organic matter. Loss of aggregation from the destruction of organic matter binding mineral soil particles decreases pore volume and impedes flow of air and water through the soil. Decreased porosity also decreases the capacity of a soil to retain water.

Fire can also create other negative hydrologic impacts such as the development of a hydrophobic layer within the upper soil horizon (DeBano et al., 1998). Often after fire a discrete water repellent layer of variable thickness develops on the soil surface to a few centimeters below the surface (DeBano et al., 1998). Water repellency results from vaporized organic compounds condensing on cooler mineral soil particles forming non-wettable coatings (Fisher and Binkley, 2000). There is a relationship between fire temperatures and water repellency formation within upper soil horizons. Below 176^{o}C little change occurs (DeBano, 1981), between 166 and 204^{o}C the greatest water repellent layer is formed (DeBano, 1981), and above 288^{o}C the hydrophobic compounds are destroyed (Savage, 1974; DeBano et al., 1976).

Structural loss and/or development of a hydrophobic layer can exacerbate erosion on steeper slopes. Loss of forest floor during fire exposes the surface mineral soil to raindrop impact. Particle detachment from raindrop impact combined with energy from increased surface runoff due to decreased infiltration and water repellency can initiate erosive events (See Chapter 11).

Chemical Soil Properties

Biogeochemical cycling of nutrients stored in SOM is critical for soil organisms and plant growth (Paul and Clark, 1996). Organic matter supplies the majority of plant available P and S in soils, and virtually all the N required by plants and soil organisms. Oxidation of SOM during fire alters nutrient pools, biological N fixation, and mycorrhizal development (DeBano et al., 1998; Neary et al., 1999, 2000).

Chemical constituents found in SOM are lost at different temperatures during forest fires (DeBano et al., 1998). Laboratory studies have shown thermal destruction of SOM begins at temperatures below 100^{o}C, with volatile constituents lost at temperatures up to 200^{o}C. Increasing temperatures between 200 and 300^{o}C results in losses up to 85 percent of organic matter. Further heating to 450^{o}C for 2 hours, or to 500^{o}C for ½ hour, can remove up to 99 percent of the organic matter (DeBano et al., 1998). Only during severe fires do temperatures approach the necessary levels to appreciably

impact the surface mineral soil C pool (Table 1), yet considerable losses do occur in the forest floor and organic horizons where the greatest concentration of combustible material resides.

Biological Soil Properties

Microbial community abundance is greatest in the forest floor and surface mineral soil layers where the highest concentrations of organic matter and fine roots (<2mm) are found (Paul and Clark, 1996). These organisms, primarily organotrophs, utilize C from plant roots, root exudates, and plant material derived from litterfall for their maintenance, growth, and reproduction (see Chapter 7). The greater abundance of microorganisms and fine roots near the soil surface expose these populations to potentially lethal temperature during a fire.

The impact of fire on the soil biota is mediated, in part, by soil water content. Thermal gradients that develop from surface fuels to mineral soil during fire are affected by soil moisture content. Water, being a better conductor of heat than air, transfers lethal temperatures to greater depth with increasing soil moisture (DeBano et al., 1998; Neary et al., 1999). Higher mortality of soil organisms occurs with greater soil moisture compared to dry conditions at the same temperature (Dunn and DeBano, 1977; Dunn et al., 1985). Another possible factor related to soil moisture is increased microbial population recovery as a result of spore formation by some microorganisms during periods of moisture stress prior to the fire (Chromanska and DeLuca, 2002).

Microbial mortality is a direct effect of soil heating to lethal temperatures (50-210^{o}C), but thermal decomposition and combustion may also deplete their energy source bound in SOM (Neary et al., 1999). Loss of soil microorganisms due to lethal temperatures can potentially alter decomposition, nutrient cycling, and nutrient uptake by plants (Paul and Clark, 1996; DeBano et al., 1998; Neary et al., 1999; Swift, 2001).

WINDTHROW

Windthrow is a natural phenomenon that describes the process by which strong winds shear or completely uproot trees. Winds can damage individual trees within a stand (Runkle, 1981, 1985; Runkle and Yetter, 1987) or blow down thousands of hectares of trees during large storms (Bormann and Likens, 1979; Peterson and Pickett, 1991). Wind damage intensity and frequency varies over a wide range in different forest types (Dunn et al., 1983; Runkle, 1985; Peterson, 2000). Examples from the literature range from 0.5 and 0.8% in two Minnesota forest types (Webb, 1988), 11% in mature southern Appalachian mixed hardwood forest (Clinton et al., 1993), to 97% in canopy gaps of mature mixed-mesophytic forests in the southeastern USA (Barden, 1981).

Wind damage not only shears and uproots trees, but also creates microtopographic variation called pit and mound formation (Beatty, 1984; Beatty and Sholes, 1988; Peterson et al., 1990, Bormann et al., 1995; Liechty, et al., 1997). The physical action of uprooting inverts soil horizons (Beatty and Stone, 1986), displaces large rocks (Lutz, 1960), and creates pit and mound pattern of micro-relief (Putz, 1983).

Small-scale variation in relief from pit and mound formation plays an important role in regenerating forest community structure and composition (Beatty, 1984, McClellan et al., 1990; Harrington and Bluhm, 2001). Clinton and Baker (2000) found that large storm events such as hurricanes primarily topple older trees with large crowns and full foliage on ridges and upper slope positions. Soil on these topographic positions tended to be shallow and easily saturated from precipitation during the storm, making older trees more vulnerable to windthrow.

Foster and Boose (1992) found a positive relationship between tree height and wind exposure causing treefall, while slope position was not a substantial factor. Exposure is a complex characteristic controlled by aspect, slope, topographic position, and landscape placement relative to obstructing barriers in the upwind direction (Foster and Boose, 1992). Others (e.g., Greenberg and McNabb, 1998) have found soil depth and slopes did not significantly influence the susceptibility of trees to uprooting; rather susceptibility to uprooting was a function of wood properties, tree morphology, rooting depth, and storm severity (i.e., amount of wind energy combined with precipitation).

Pit and mounds are characterized by distinct changes in the soil profile (Greenberg and McNabb, 1998; Beatty and Stone, 1986; Beatty and Sholes, 1988; Bormann et al., 1995; Peterson, 2000). The type of treefall dictates the

morphology of pit and mounds. Two basic pit and mound patterns, hinge and rotational, have been described based on location of the tree bole and root mat with respect to the pit and the pattern of redistribution of surface organic matter and subsoil (Beatty and Stone, 1986).

Initially, pits lose the litter layer and upper mineral soil horizon when the tree is uprooted. Organic debris from the upturned forest floor is typically little disturbed, yet some may be deposited within the pit. Mound structure is very dependent on the durability of the upturned basal roots. The rate of decomposition of the root mass determines the degree of mixing of subsoil and surface soil and formation of the mound (Beatty and Stone, 1985). Pits fill in relatively quickly compared to the rate at which mounds dissipate. Over time, mounds become the primary distinguishing feature (Beatty and Stone, 1985).

Pits often become saturated with water slowing decomposition, while mounds drain more freely (Beatty and Stone, 1985; Liechty et al., 1997). Pits and mounds create microclimate variation, causing differences in soil moisture, aeration, and temperature over relatively short horizontal distances (Beatty and Stone, 1985). Clinton and Baker (2000) reported the following distribution pattern for organic C at Coweeta Basin in North Carolina one year after a windthrow event: 2.15% mound, 2.11% pit wall, 1.42% pit bottom, and 4.73% in the undisturbed area. Beatty and Stone (1985) report organic matter distribution as 5.7% (3.31% C) for mound, 17.8% (10.32% C) for pit, and 10.0% (5.8% C) for undisturbed sites at the Huyck Preserve in New York. Data from Huyck Preserve was compiled from 48 sites with ages of <30 years to approximately 200 years since the windthrow event.

Bormann et al. (1995) characterized mechanisms of change in mounds of southeast Alaska following windthrow events from three age classes within three Sitka spruce (*Picea sitchensis* (Bong.) Carr.)-western hemlock (*Tsuga hererophylla* (Raf.) Sarg.) forests. The initial age class (0-50 years) accumulated organic matter in surface mineral soil along with deep rooting into the soil profile, while C losses occurred in the disturbed O and Bh horizons. During the second stage (50-200 years), C accumulated through the entire soil profile with the greatest accretion in the Bh horizon while the amount of rooting in the mineral soil persisted. The oldest sites within this chronosequence appeared to accumulate C at comparable rates as the previous phase.

Extrapolation of mound dynamics past 350 years projected increased C and N forest floor accumulations, with shifts in rooting from the mineral soil to the O horizon. Soil C dynamics in this region are characterized by rapid decomposition after disturbance followed by periods of accumulation (Bormann et al., 1995). The accumulation of soil C is dependent on frequency of windthrow events and the type and amount of organic matter inputs. Increased frequency of events prevents thick organic horizon accumulation and immobilization of plant nutrients, which could lead to decreased primary productivity.

In regions where fire is rare, windthrow is often the predominant natural disturbance (Bormann et al., 1995). The redistribution of forest floor, bark, log and stumps, and other organic debris create very different opportunities for plant regeneration depending on soil properties, type of tree fall, and storm frequency and severity (Beatty and Stone, 1985; Ulanova, 2000). Mixing of mineral soil and forest floor can increase decomposition and release of nutrients. Extended periods without windthrow in these ecosystems can lead to altered succession (i.e. bog formation in northern latitudes) and accumulation of considerable organic matter albeit less productivity. Forests that have evolved with windthrow may exhibit greater ecosystem productivity (Bormann et al., 1995), with minimally altered forest floor and soil C storage over long-term periods (Liechty et al., 1997) if disturbance occurs within the range of natural variability.

FOREST INSECTS AND PATHOGENS

Insects and pathogens are important components of forest ecosystems, considered disturbance agents only when they cause tree mortality, wood decay, or defoliate trees at an ecosystem scale (Dahms and Geils, 1997). The relationship between insect irruptions and stand condition is interactive in that forest stand condition affects the distribution and reproduction of insects and pathogens, and insect and pathogen populations and distributions affect stand condition. Impacts to soil C pools from insect and pathogen disturbances over landscape scales is unknown.

Tree mortality resulting from insects, fungi, and parasitic plants are limited by availability to susceptible hosts (Dahms and Geils, 1997). Swetnam and Lynch (1993) found that western spruce budworm outbreaks historically affected the composition and structure of western coniferous forests, resulting in spatially heterogeneous stands of host and non-host species. They found that outbreaks during the 20th century have become less frequent but more severe with respect to tree growth reduction. They attributed this to changes in forest structure caused by extensive logging during the early part of the 20th century followed by favorable climatic conditions, fire suppression, and reduced sheep grazing allowing greater seedling establishment of potential hosts. Another finding of their study is that climatic conditions that decrease plant stress often can trigger insect outbreaks as readily as climatic conditions that increase plant stress. For example, forests in arid areas may be more susceptible to insect outbreaks during high precipitation years while forests in more humid regions become vulnerable during drought conditions.

The interaction among disturbance agents plays a key role in the severity of disturbance. Baker and Veblen's (1990) analysis of mortality patterns in subalpine forests of Colorado suggest that insect outbreaks in this region may play as key a role in mortality as fire. Fire had always been considered the primary disturbance agent, but their investigation shows a sequence of different disturbances (fire, insect outbreaks, windthrow) shaping the landscape vegetation structure created over century scales. Similar findings demonstrate increases in bark beetle populations in the Rocky Mountain West influenced by long-term drought, windthrow, snow and ice damage, landslides and avalanches, and fire (Veblen et al., 1994). Bark beetle outbreaks alter forest stand densities, while increasing coarse woody debris and forest floor accumulations.

Whether insect or disease, the impact on forest ecosystems is reduced tree growth with decreased leaf and root inputs to the forest floor and soil. Reduced tree growth and mortality affect net primary production by decreasing the capture of energy by photosynthesis. Production loss from tree mortality can be rapidly offset by regeneration of seedlings and herbaceous understory as nutrients and soil moisture are released following disturbance. How quickly production resumes and at what level can be greatly influenced by severity and duration of the insect or pathogen outbreak.

The succeeding vegetative community directly affects soil C dynamics.

DROUGHT

Drought is a meteorological term that means a lack of precipitation over a prolonged period of time. During the 20th century, three major droughts (1933-1940, 1951-1956, 1987-1989) severely impacted the United States (Cook et al., 1999). Drought creates water stress in plants, with extended periods of water stress causing mortality due to desiccation. Some plants possess mechanisms of resistance to prevent or slow water loss in certain tissues or organs, or they possess the ability to increase rates of absorption and translocation of water (Hale and Orcutt, 1987). These attributes have been selected for in drought-prone regions, but where drought is infrequent the impact of drought on the community can be severe.

Drought decreases C input into the soil due to reduced net primary production (Gower et al., 1992; Cregg and Zhang, 2001). Photosynthesis, nutrient uptake, growth, and reproduction of plants require a continuous flux of water absorbed from the soil (Porporato et al. 2001). Drought may reduce leaf area (Boyer, 1988) and net photosynthesis (Chaves, 1991) of a tree. Leaf area index in forest stands determines annual growth potential, but is sensitive to moisture stress (Gower et al., 1992).
One strategy of drought avoidance is the allocation of fixed C to deep roots over canopy production aiding water flux (Williams et al., 2001). Deep roots are more resistant to decomposition due to the quality of C (lignin) compared to leaf litter (cellulose, hemicellulose). The decreased above-ground organic matter inputs of readily available C plus the increased resistant C from deep roots resulting from drought stress alters C dynamics by changing the rate of C turnover in mineral soil.

Visible affects from drought are obvious in the vegetative community, but water stress also affects soil microbial communities (See Chapter 7). Microbial activities have been shown to fluctuate with available soil moisture, typically measured by rates of decomposition (Potts, 1994; Paul and Clark, 1996). Some microorganisms can tolerate long periods of desiccation by forming spores that allow them to

persist until adequate moisture triggers germination, growth, and reproduction (Skujins, 1984).

Drought alters the quality and quantity of C pools within the soil by decreasing input of more readily decomposable leaf litter to the forest floor with greater photosynthetic C allocated to lower quality C in roots. Altered C inputs and reduced microbial activity during moisture stress reduces decomposition, which should result in reduced total soil C accumulation and increased turnover time of SOM. The accumulation of SOM depends not only on quantity and quality litter inputs, but also on the rate of decomposition. The inter-relationship between microbial resilience and drought severity over large spatial scales on C pools in soils is not available.

Complicating measurement of drought affects is interaction between drought severity, fire (Barton et. al., 2001; Sherriff et al., 2001), and insect outbreaks (Cochran, 1998). As with all disturbance agents the spatial and temporal scales can vary widely with ecosystem affects proportioned to the severity of the events and resilience of the system.

CONCLUSIONS

Forest management early in the 20th century focused on economics. Efforts to mitigate and suppress negative disturbance effects on potential production were emphasized. With implementation of numerous environmental laws, changing public attitudes, and growing body of knowledge, management has shifted its focus from potential production to sustaining ecosystems over long time periods. Conservation of biodiversity has become important, which includes not only preserving individual species, but also preserving the diverse mosaic of forest communities and those ecosystem processes that make these communities unique.

Forests ebb and flow with natural disturbance, in turn forest C dynamics oscillate with changing conditions, altering pools sizes and transfer rates, eventually converging toward a level of C storage influenced by physical conditions such as climate. As C accumulates over time, the likelihood of more severe impacts from disturbance increases. Accurate and precise assessment of spatial heterogeneity in soil C storage is essential for evaluating the impact of disturbance on forest soil C pools. Currently meta-analysis of disturbance effects on soil C dynamics does not support the notion of decreased total soil C resulting from natural disturbance events. However, this result may be due to the difficulty is assessing soil C change over time in a spatially complex system. More research is needed to definitively characterize the short- and long-term effect of disturbance on forest soil carbon, and to identify opportunities to minimize carbon loss, or maximize carbon sequestration, as a result of disturbance.

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Table 1. Fire severity classification based on postfire appearances of forest floor and mineral soil, and soil temperature profiles (Adapted from DeBano et al., 1977; Neary et al., 1999).

	Fire Severity		
Parameter	Low	Moderate	High
Forest floor temp.	250°C	400°C	675°C
Temp. 0-25 mm-mineral soil	100°C	175°C	190°C
Temp. 25-50 mm-mineral soil	<50°C	50°C	75°C
Upper forest floor (O_i)	Partially consumed	Mostly consumed	Totally consumed
Lower forest floor ($O_a + O_e$)	Intact, surface char	Deep char/ consumed	Consumed
Forest floor woody debris-small	Partly consumed, charred	Consumed	Consumed
Forest floor woody debris-large	Charred	Charred	Consumed, deeply charred
Ash color	Black	Light colored	Reddish, orange
SOM 0-25 mm-mineral soil	Pyrolysis begins	Partially scorched	Consumed/scorched
SOM 25-50 mm-mineral soil	Not affected	Pyrolysis begins	Pyrolysis begins
Roots-forest floor	Killed	Killed	Killed
Roots 0-25 mm-mineral soil	Killed	Killed	Killed
Roots 25-50 mm-mineral soil	Not affected	Not affected	Killed
Microorganisms-forest floor	Killed	Killed	Killed
Microorganisms 0-25 mm-mineral soil	Not affected	Selective die-off	Killed
Microorganisms 25-50 mm-mineral soil	Not affected	Selective die-off	Killed
Volatized nutrients-forest floor	N	N, organic P	N, K, P, S
Volatized nutrients 0-25 mm-mineral soil	None	None	None
Volatized nutrients 25-50 mm-mineral soil	None	None	None