INFLUENCE OF SOIL ORGANIC MATTER ON FOREST PRODUCTIVITY*

D. F. GRIGAL

Department of Soil, Water, and Climate,
University of Minnesota, St. Paul, Minnesota 55108, United States

and E. D. VANCE

National Council for Air and Stream Improvement Inc.,
P.O. Box 13318, Research Triangle Park, N.C. 27709-3318, United States

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ABSTRACT

Soil organic matter (SOM) is generally assumed to be important to forest productivity, but its direct influence has been difficult to clearly demonstrate. SOM has a myriad of interactions with other soil properties, and levels of SOM depend on plant factors such as productivity and litter chemistry, and on environmental factors such as temperature and water. SOM is thus both cause and effect with respect to productivity. Additionally, SOM is inversely related to productivity where conditions such as low temperatures or reduced aeration are adverse for both plant growth and for microbial activity, and SOM accumulates. Conventional experimental methods are unlikely to provide a wholly-inclusive general demonstration of the effects of SOM on forest productivity because the relationship is complex and site-specific. In spite of that caveat, circumstantial evidence indicates that SOM positively affects long-term forest productivity, with its specific role and contribution depending on the limiting site factors. In coarse-textured soils, SOM is important for retaining water and for supplying and retaining nutrients. As soils become finer, those roles become less important but its role in promoting favourable soil physical properties increases. Forest management practices can alter the amount and type of SOM, but because inherent soil or site characteristics sometimes compensate for or mitigate the effects of SOM change, the direct impacts on productivity may be equivocal. Nonetheless, because of the strong ties of SOM to a wide range of soil properties and functions across soil textures, most prudent forest management regimes should maintain or enhance SOM levels.

Keywords: soil carbon, soil quality, sustainability

INTRODUCTION

Forest growth is influenced by biological factors, including genetic variation, insects and disease, and inter- and intra-specific competition for resources; by climate, including length of the growing season and the temperature and precipitation regimes during that season; and

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by site characteristics, including topographic and soil properties. Soil organic matter (SOM) is generally positively related to forest productivity, and it can be affected by forest management (Johnson 1992a). In some cases SOM influences productivity by enhancing soil physical properties for plant growth, in other cases by enhancing fertility, and in other cases its precise role is uncertain. The strength of the relationship between SOM and forest productivity has important implications for forest sustainability. Recent literature reviews dealing with forest systems have strongly emphasised the importance of SOM to productivity (Henderson 1995; Jurgensen *et al.* 1997; Powers *et al.* 1990), although some reports have not found that relationship (e.g., Edmonds & Chappell 1994). A key question, therefore, is whether there a *direct* link between SOM and forest productivity, or whether SOM is merely important as a covariate whose role can be supplanted by other soil properties.

Because of the generally positive relationship of SOM to productivity, SOM is often used in assessing soil quality, "The capacity of a soil to function within ecosystem boundaries to sustain biological productivity, maintain environmental quality, and promote plant and animal health," (Doran & Parkin 1994, p. 7). Many soil properties that have been suggested as measures of quality are directly or indirectly linked to SOM, such as total organic carbon (C)) and nitrogen (N), labile organic carbon, microbial biomass carbon and nitrogen, potentially mineralisable nitrogen, soil respiration, and the ratio of microbial biomass carbon/total organic carbon (Doran & Parkin 1994; Larson & Pierce 1994). As a reflection of its perceived importance, SOM is one of the indicators used in the Montreal Protocol, an international set of indicators of sustainable forest management (Ramakrishna & Davidson 1998). Thus, there is a continuing focus on SOM with respect to soil quality, whether related to sustained productivity, biodiversity, or other ecosystem attributes.

BASIC RELATIONSHIPS

The soil properties that affect forest productivity are those providing a suitable environment for and adequate quantities of water and nutrients to roots, the interface between the soil and the plant. Succinctly, "Site quality is largely determined by soil properties, or other features of site, which influence the *quality* and *quantity* of growing space for tree roots" (Coile 1952). Soil properties, including SOM, are commonly inter-related, and these relationships are so strong that it has been suggested that a major source of variation in soil properties is simply the amount of organic matter (Federer *et al.* 1993). The inter-relationships between soil properties and SOM can be expressed qualitatively, and *pedotransfer functions* (Bouma 1989) express those relationships quantitatively. These are statistical or empirical functions used to relate soil characteristics with one another and to estimate soil properties that are too difficult or expensive to measure directly.

Physical Properties

Soil aggregation, the coherence of particles into discrete peds or structural units, is strongly influenced by SOM (Rawls *et al.* 1991). The resulting relative volume of solids and voids and the pore-size distribution affects the capacity of the soil to transport and store water and gases. Tree roots, living organs, require both water and adequate oxygen for aerobic respiration. Soil bulk density, an indirect measure of the volume of solids and voids, is therefore related to the quality of a soil for root growth. Roots also require a medium into and through which they can grow without major impediment. Soil strength, which can limit root penetration even in soils with adequate aeration (Unger & Kaspar 1994), increases with increasing bulk density and with decreasing water content (Unger & Kaspar 1994) (Fig. 1). Bulk density is therefore a key soil property affecting both the quality (aeration) and the quantity (penetrability) of root growing space. This is recognised by development of such indices as the "growth-limiting bulk density", above which root growth essentially stops (Daddow & Warrington 1983).

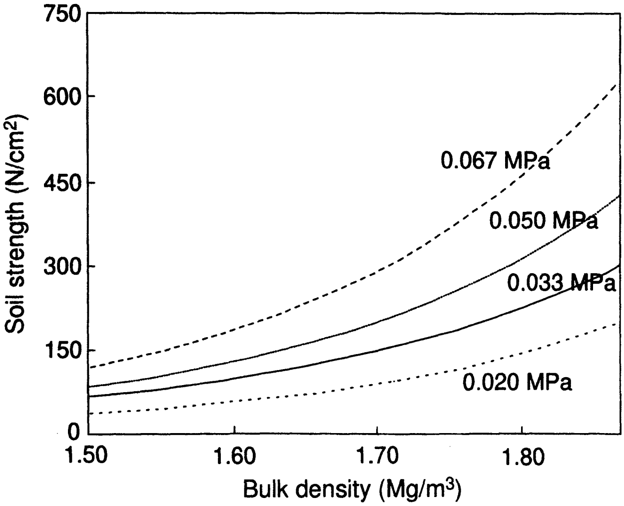

FIG. 1–Relationship between soil bulk density, water potential, and soil strength (from Taylor & Gardner 1963; redrawn by Unger & Kaspar 1994). Data from a laboratory study using fine sandy loam soil, compressed to desired bulk densities, and with water potential controlled.

The bulk density of most surface soils is closely related to SOM; a relatively small increase in SOM in soils with low SOM leads to a large decrease in bulk density, while in soils with higher SOM density changes more slowly. Pedotransfer functions quantifying this relationship are similar, whether the data were collected in forests in New England (Curtis & Post 1964), England (Jeffrey 1970; Adams 1973), California (Alexander 1980), or the Lake States (Grigal *et al.* 1989) (Fig. 2). Histosols, organic-rich soils, have similar functional relationships, albeit with different statistics (Grigal *et al.* 1989). Soil compactibility is also reduced by SOM (Zhang *et al.* 1997), making soils more resilient with respect to management activities.

Another important attribute of the rooting environment is water retention. Many pedotransfer functions relate water retention to other soil properties including soil texture, SOM or organic carbon, and bulk density (Shaykewich & Zwarich 1968; Gupta & Larson 1979; Rawls *et al.* 1982; De Jong *et al.* 1983; Rawls *et al.* 1983, 1991). Based on these functions, retention of available soil water increases with SOM in spite of concurrent decreases in soil bulk density (Fig. 3). SOM is thus important in maintaining soil physical conditions in a range suitable for root growth.

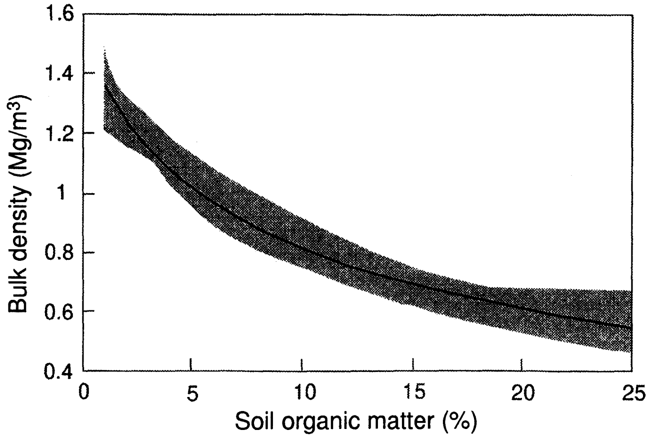

FIG. 2–Relationship between soil bulk density and SOM. Shaded area indicates range of predictions from equations based on data collected in New England (Curtis & Post 1964), England (Jeffrey 1970; Adams 1973), California (Alexander 1980), and the Lake States (Grigal *et al.* 1989). The line, the best-fit of those predictions, is described by BD (Mg/m^3) = EXP [0.23 – 0.037 × SOM (%)], where BD is bulk density and SOM is soil organic matter.

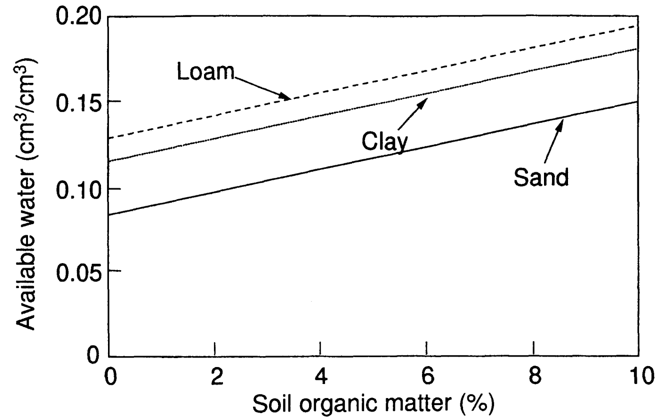

FIG. 3–Relationship between available water retention and SOM. Mean of predictions from equations from Shaykewich & Zwarich (1968), Gupta & Larson (1979), Rawls *et al.* (1982, 1983), and De Jong *et al.* (1983). The lines are described by AW (cm^3/cm^3) = 10^{-3} × [11.72 × SOM (%) + 0.06 × CL (%) – 0.89 × S (%) + 133.5 × BD (Mg/m^3)], where AW is available water retention, SOM is soil organic matter, CL is clay, S is sand, and BD is bulk density. Available water is defined as the difference between water retained at 33 kPa (1/3 bar) and at 1.5 MPa (15 bar).

Chemical Properties

In addition to influencing soil physical properties, SOM also influences chemical properties. Nutrients that occur primarily as cations (calcium (Ca), magnesium (Mg), and potassium (K)) are retained by negatively-charged exchange sites, including soil clays and

SOM. Although the cation exchange capacity (CEC) of clays is usually emphasised, SOM is important in many forest soils because they are relatively low in clay. The CEC of SOM increases with pH (Helling *et al.* 1964; Kalisz & Stone 1980), and forest soils vary in and are often low in pH. As a result, the reported CEC of SOM in forest floor varies from about 20 to 55 cmol_c/kg of organic matter, and in mineral soil from 40 to 165 cmol_c/kg (Mader 1953; Hoyle 1973; Kalicz & Stone 1980; Ross *et al.* 1991; Santore *et al.* 1995; Grigal unpubl. data). In spite of that range, SOM is clearly important in retaining cations.

Rates of weathering, the dissolution of minerals, and subsequent release of constituent ions, are enhanced by SOM. Organic acids associated with SOM (e.g., Boyle & Voigt 1973) act as ligands by forming complexes with mineral surfaces (Bloom & Nater 1991) and reduce the activities of some mineral components (Boyle *et al.* 1974), in both cases increasing rates of weathering. Conversely, mineralisation of SOM, described below, may also release elements in solution and increase their chemical activities, slowing weathering (Zabowski *et al.* 1994). The difficulty of clearly isolating the role of SOM in ecosystem processes is illustrated by its multiple and counteracting roles in weathering.

Biological Properties

Soil organisms play a vital role in decomposing organic matter, releasing inorganic forms of nutrients available for plant uptake (i.e., mineralisation), and enhancing soil structural characteristics important for maintaining adequate soil water and air relations. The vast majority of soil organisms are heterotrophs, depending on SOM for carbon and energy. Activities of soil biological communities are strongly affected by physical and chemical properties related to SOM, and they also feed back to influence those properties. Usually, the functioning of the entire microbial population is more relevant for addressing questions of sustainable site productivity than is its composition. Carbon in microbial biomass comprises 1–3% of total soil organic carbon across a range of vegetation and soil types (Jenkinson & Ladd 1981; Vance *et al.* 1987; Martikainen & Palojärvi 1990; Wolters & Joergensen 1991; Sparling 1992), and a close relationship appears to exist between microbial biomass and the rapidly cycling fraction of SOM (Janzen *et al.* 1992). Quantities of carbon and nitrogen within microbial biomass have been directly related to above-ground net primary production across a range of forests and other ecosystems in North America (Myrold *et al.* 1989; Zak *et al.* 1994). While they do not directly decompose SOM, soil fauna are closely linked with the soil microbial community in organic matter decomposition, nitrogen and phosphorus mineralisation, and soil structural development (Lavelle 1997). Fauna influence mineralisation by grazing on fungi and bacteria, serving as their food, and dispersing fungal inoculum (Lussenhop 1992).

Mineralisation

Essential plant nutrients in SOM, derived from living material, are released by mineralisation and can be used by plants, adsorbed within the soil, or become susceptible to hydrologic losses. Literally hundreds of studies of mineralisation have been widely reviewed and synthesised (e.g., Binkley & Hart 1989; Gressel & McColl 1997; Johnson 1992b, 1995), and we will simply re-emphasise some of the key points with respect to SOM. Nitrogen release via mineralisation is usually emphasised (Johnson 1992b) because (a) virtually the entire pool of nitrogen in forests is organically bound, (b) nitrogen availability is low relative to plant uptake, and (c) additions of nitrogen via fertiliser application increase tree growth in most forests. Annual nitrogen mineralisation statistically explains virtually all of the variation in productivity in some systems (e.g., Lennon *et al.* 1985; Nadelhoffer *et al.* 1985; Pastor *et al.* 1984; Zak *et al.* 1989; Reich *et al.* 1997). Because of the complex interactions among SOM, microbes, and other environmental factors, and because rates of mineralisation and the total quantities of mineralised nitrogen are both affected by the same environmental factors that influence plant growth, such relationships should not be considered simple cause-and-effect. For example, in Scandinavian systems with the same lodgepole pine (*Pinus contorta* Dougl.) cover type, site productivity was most strongly related to temperature variables, especially the length of the growing season (Fries *et al.* 1998). The positive relationship of temperature to nitrogen mineralisation may explain this observation, but nitrogen availability (Yin 1992) and nitrogen concentration in foliage (Yin 1993) and fine roots (Yin & Perry 1991) appear to decrease with increasing temperature. This indicates that at higher temperatures available nitrogen is more fully used by trees, leading to reductions in soil concentrations and a dilution in plant tissue.

Forest productivity is often limited by phosphorus availability (Gressel & McColl 1997). As a legacy of the agronomic background of soil science, including a short-term (annual) view of nutrient availability and an emphasis on inorganic fertilisers, available soil phosphorus is usually considered to be primarily affected by inorganic compounds. The importance of organic phosphorus has been demonstrated in many forest systems, because of both a longer-term perspective and continuous nutrient cycling (Kelly *et al.* 1983; Turner & Lambert 1988; Bekunda *et al.* 1990; Polglase *et al.* 1992). Sulphur is another essential plant nutrient that is closely linked to SOM (David *et al.* 1995), and its availability is a concern for some sites in the Pacific Northwest (Edmonds & Hsiang 1987) and in the Southern Hemisphere, often where fertiliser application has increased availability of other nutrients. In most of North America and Europe, atmospheric deposition supplies adequate sulphur for plants (Johnson 1984), but because the magnitude of these inorganic inputs is relatively independent of either the nitrogen or phosphorus status of the system, the stoichiometric ratios of sulphur to either phosphorus or nitrogen among vegetation components and species are more variable than are ratios between phosphorus and nitrogen (Homann & Harrison 1992).

Mineralisation is fundamentally a microbial process, and is influenced by factors affecting microbial activity including pool sizes, characteristics of the organic matter, and environmental conditions. The link between climate and rate of litter decomposition is well-documented (Meentemeyer 1978; and others), as is that between climate and mass of SOM (Grigal & Ohmann 1992; Homann *et al.* 1995; Johnson 1995; Gärdenäs 1998; and many others). Nitrogen mineralisation may be limited by environmental conditions. Although about 10% of the total organic nitrogen in SOM in Lake States' forests is potentially available for release (Zak *et al.* 1993), only about one-fourth of that fraction is annually released in the field (Reich *et al.* 1997). The composition of the organic matter is also important, with nitrogen release linked to concentrations of nitrogen and lignin, the latter operationally defined as residue following a sulphuric acid extraction of fresh litter (Berg 1986). This emphasis on lignin contrasts to the traditional emphasis on the C:N ratio (Stevenson 1986), but lignin:nitrogen has been recognised in both simple algorithms (Meentemeyer 1978) and in more complex modelling systems (Schimel *et al.* 1994). Additions of nitrogen to organic material, especially recalcitrant materials with high C:N ratios such as those typically found in forests, may even have a negative effect on rates of decomposition (Fog 1988). This influence of organic matter composition on decomposition is illustrated in the Lake States, where mass of SOM in the upper metre of soil ranges over 50% with forest type (Grigal & Ohmann 1992), and in Scandinavia where the single most important factor determining mass of organic matter in forest floor is overstorey genera (Gärdenäs 1998).

Biochemical inhibition/enhancement

SOM can also directly inhibit or enhance growth. *Allelopathy* is defined as "... any direct or indirect harmful effect by one plant (including micro-organisms) on another through the production of chemical compounds that escape into the environment" (Rice 1977, p. 201). Allelopathic effects may prevent seed decay, affect seed and bud dormancy, promote infection by pathogens, increase resistance of plants to disease, influence the patterning of vegetation, inhibit nitrification, and influence plant succession (Rice 1977). As a pool of organic compounds, SOM is an intermediate in this phenomenon. Although allelopathy can influence tree growth and response to management, it is usually species- and site-specific and hence will not be further discussed. Documented evidence also exists for positive effects of humic substances, derived from SOM, on plant growth (Chen & Aviad 1990). Although some of this enhancement is related to indirect effects such as the solubilisation of micronutrients and enhancement of microbial populations, some direct effects include the positive influence of humic materials on root membranes and enzyme activity and their hormonal-like effects (Chen & Aviad 1990). Although it is likely that some of these effects occur in forests, nearly all studies have been carried out with agronomic plants in the laboratory or growth chamber. Clear demonstrations of these effects in the field are unlikely because of the multiple interactions of SOM in soil-plant relationships.

Conclusions

This brief excursion into basic relationships emphasises the fact that SOM has many roles in forest ecosystems. It is an important soil property and it affects and is affected by many other soil properties; although it may affect forest productivity, it is also affected by it. As a result of these complexities, evidence for the influence of SOM on forest productivity is likely to be primarily circumstantial.

FOREST FLOOR

Forest floor, an important and unique component of SOM in forested systems, reflects the balance between system production and decomposition. It includes "... all organic matter, including litter and decomposing organic layers, resting on the mineral soil surface ..." (Pritchett & Fisher 1987), and is often referred to as "forest humus" in the older literature (Wilde 1946). Forest floor influences the temperature, aeration, moisture status, and nutrition of the rooting zone, and has a significant impact on many ecosystem characteristics and functions including (1) reproduction of vegetation, (2) susceptibility to erosion through protection of surface soil, reduction of raindrop impact and splash, and enhancement of water infiltration rates, (3) fuel type and fire behaviour, (4) microflora and microfaunal activity and their role in nutrient cycling, (5) soil aggregation and structure, and (6) susceptibility to disease. It is therefore very important to long-term forest productivity.

Morphology

In the late nineteenth century, Müller focused attention on two distinct endpoints in the continuum of surface organic horizons and organic-enriched mineral horizons in beech (*Fagus* spp.) forests in Denmark (Handley 1954). He termed one endpoint the *mor* humus form or type, where organic matter accumulates at the soil surface, and the other endpoint the *mull*, where organic matter is intimately incorporated into the upper mineral soil by fauna, predominantly earthworms, or by root systems of herbs or graminoids (Green *et al.* 1993). Intermediate states, termed *moder* or *duff mull*, combine organic accumulations with some incorporation into mineral soil. Mors are commonly considered to represent "slow decomposition processes" and "a storage of nutrients which are slowly released and made available to plants", and mulls are characterised by "rapid decomposition and mineralisation of organic materials" (Green *et al.* 1993). The forest floor type is not a permanent feature of a site; it can change with forest changes such as succession or disturbance (Handley 1954).

Dynamics

Steady-state

Although all functions of forest floor are important to forest productivity, attention has focused on the balance between inputs and outputs, and the resulting sequestration or release of plant nutrients. The simplest case is a forest floor in steady-state where inputs and outputs are approximately equal and mass is neither increasing nor declining (Olson 1963; Minderman 1968). Olson (1963) suggested a simple "decomposition rate factor", *k*, as the ratio of mass of annual litter production to that of steady-state forest floor. The ratio ranged from approximately 4 for moist tropical systems to 1/64 for high-elevation coniferous systems, and Olson (1963) inferred a positive relationship between the magnitude of the ratio and productivity; systems with high ratios are "highly productive", and vice versa. By implication, high *k*'s indicate a mull type of forest floor and low *k*'s a mor.

Although *k* may be related to organic matter turnover and nutrient cycling, it cannot fully explain differences in productivity. In steady-state, the annual loss of material from the forest floor via decomposition must be equal to the annual addition via litterfall and there is little *net* change in forest floor mass or nutrients. In those cases, differences in forest floor type do not reflect differences in net nutrient flux, and hence presence of mor or mull should not translate into differences in site productivity. For example, nearly all of the annual nutrient demand of a closed-canopy loblolly pine (*Pinus taeda* L.) plantation could be satisfied by annual mineralisation of the mor forest floor (Jorgensen *et al.* 1980). In another case, invasion of earthworms over a 14-year period converted a mor to a mull in an aspen (*Populus tremuloides* Michx.)stand. Despite a decline of about 85% in the mass and thickness of the forest floor, there was no measurable change in site productivity (Alban & Berry 1994).

Another example where forest floor type and productivity did not conform to the axiomatic model occurred in sugar maple (*Acer saccharum* Marsh.) stands in Quebec. Phosphorus deficiency, demonstrated by differences in foliar phosphorus concentrations and associated visual deficiency symptoms linked to tree dieback, occurred in stands on mulls but not in stands on mors (Paré & Bernier 1989). In spite of this observation, pools of total phosphorus, organic phosphorus, and inorganic phosphorus on mors were only about one-sixth of those on mulls. This perplexing result was ascribed to efficient mineralisation and subsequent tree uptake of phosphorus in the mors, whereas phosphorus in mulls was fixed in unavailable forms by iron and aluminum oxides in the mineral soil fraction (Paré & Bernier 1989). Although systems with different *k*'s may differ in productivity, these differences cannot be equated to differences in the nutrient dynamics of the steady-state forest floors; the same factors that affect *k* also affect productivity.

The inference that high *k* implies high productivity also neglects below-ground inputs to the forest floor; the ratio (*k*) is based only on litterfall (Olson 1963). Below-ground inputs, especially from fine roots, may be substantial (Ehrenfeld *et al.* 1992; Vogt *et al.* 1991) and differ among forest types (Hendricks *et al.* 1993). Although their omission in calculating *k* may not be a serious problem, it demonstrates that the ratio should not be interpreted as an overarching indicator of ecosystem productivity. In summary, although rates of organic matter and nutrient turnover are very important to forest stand nutrition, inferences based on observations of forest floor morphology should be viewed warily.

Recovery from disturbance

Although the concept of forest floor steady-state may be heuristically valuable, forest floors are more likely to be accumulating after disturbances such as fire (Viro 1969; Ohmann & Grigal 1979; Wardle *et al.* 1997), mechanical clearing (Ovington 1954), and site preparation (Morris & Miller 1994). Following afforestation, the rate of forest floor accumulation decreases with time, indicating an approach to a steady-state (Ovington 1954). Under such conditions, conifers generally accumulate a greater forest floor mass and are more likely to produce mor types than are broadleaf deciduous species (Ovington 1954). Afforestation may be an extreme case, but more subtle changes in species composition via succession can also change amounts of forest floor and rates of accumulation. In Mississippi, an initial increase in forest floor over about 100 years under pine was followed by a decrease with changes to hardwoods (Switzer *et al.* 1979).

The effect of harvesting on forest floor mass is variable and depends on site conditions, residue management, and site preparation practices (Johnson & Curtis in press). A frequently-cited study, based on 14 northern hardwood stands in New Hampshire that varied with time since clearcut harvest, reported a rapid initial decline in forest floor, over 50% within 15 years of cutting, and then a slow recovery to pre-harvest levels within 65 years (Covington 1981). The measured change in forest floor of 13 similar stands over 15 years did not conform to that predicted trajectory, and was variable among stands (Yanai *et al.* in press). Similarly, 8 years (4 years on one site) after clearcutting of three geographically-separated aspen stands in Minnesota and Michigan there was no "... evidence that forest floor weights were declining to some minimum 15 years or so after harvesting ..." (Alban & Perala 1990, p. 382) nor was there such a pattern in total carbon in forest floor and the surface mineral soil (to 25 cm) (Alban & Perala 1990). Similar results, lack of decline in forest floor mass after harvesting, are common (Wallace & Freedman 1986; Huntington & Ryan 1990; Johnson *et al.* 1991). The assumption that forest floor mass is likely to decline following harvest is clearly not generally appropriate.

Excess accumulation

The inference that accumulations of forest floor are associated with lower productivity may be based on situations where accumulation continues without reaching steady-state. An extreme example is peatlands, where organic matter (peat) accumulates because lack of oxygen due to saturation inhibits microbial activity (Gore 1983). Restricted aeration limits rooting volume and nutrients are sequestered in the peat, resulting in forests with low productivity. Lowering the water table allows gas exchange, increasing rooting volume and releasing nutrients through microbial activity (Päivänen 1997). Low temperature can also lead to forest floor accumulation and low productivity as demonstrated in the taiga of Alaska (Van Cleve & Dyrness 1983). Fire, a common disturbance, reduces both mass and thickness of the forest floor and increases available nutrients because of near-instantaneous mineralisation of organic material, increasing net primary production of vascular plants. Over time (ca. 150 years), however, a positive feedback of low temperatures that inhibit microbial activity lead to an accumulating forest floor with insulating properties that result in further accretion and reduced productivity (Van Cleve *et al.* 1983).

Ericaceous plants are associated with continuous forest floor accumulation and low forest productivity (de Montigny & Weetman 1990). Effects are well documented for a variety of species (*Calluna vulgaris* (L.) Hull (Read 1984), *Kalmia angustifolia* L. (Titus *et al.* 1995), *Gaultheria shallon* Pursh. (Weetman *et al.* 1990), and *Empetrum hermaphroditum* Hagerup (Nilsson 1994)), and the commonality of symptoms and taxonomic groups argues for similar processes. Those processes include production of phenolic acids that stabilise proteins in humus, slowing mineralisation of nitrogen and phosphorus (Bradley *et al.* 1997), development of very low soil pH through both production of organic acids and release of H+ (Read 1984), and the disruption of membranes of tree roots and associated mycorrhizas (Glass & Dunlop 1974). The result, a substantial "growth check" of associated conifers, may be temporarily alleviated by fertiliser application, or treating the ericaceous species with herbicides, or by disrupting the forest floor/root system through ripping or disking. Longer-term amelioration has been only marginally effective (Titus *et al.* 1995; Weetman *et al.* 1990).

Continuous forest floor accretion has also been reported in fast-growing, often exotic pine plantations. The specific cause of accumulation over three rotations of *Pinus patula* Schldl. et Cham. in Swaziland was difficult to discern but it was positively related to elevation and negatively related to soil properties including exchangeable calcium in the surface mineral soil (Morris 1995). Response to fertiliser indicated nitrogen limitations due to the accumulation (Morris 1995). In South Africa, both fire control and nutritional problems were related to litter accumulation beneath *Pinus pinaster* Aiton (de Ronde 1984). Increased accumulation was related to increased stand age and site index measured prior to the development of the nutritional problems. In New Zealand, forest floor accumulation in first- and second-rotation *Pinus radiata* D. Don plantations was related to a large array of environmental, stand, and soil variables including elevation (positive), winter rain (negative), and foliar calcium (negative) (Carey *et al.* 1982).

All these cases of forest floor accumulation associated with low or declining productivity are linked by an inhibition of microbial activity that leads to slowing of rates of mineralisation and consequent reduced nutrient availability and deficiencies. Although in general SOM is positively related to forest productivity, these are examples of "too much of a good thing."

Final note

There is clearly a wide-spread assumption in forest science that higher rates of forest floor turnover are associated with higher productivity. Direct links between forest floor turnover and productivity have been demonstrated only where systems are far from steady-state. Where there is excess accumulation of forest floor, rates of forest floor turnover are slowed by the same environmental factors that reduce plant growth, including adverse temperature and water. At the other extreme, near-instantaneous turnover of forest floor via fire can release available nutrients and can enhance short-term productivity. Most systems are more nearly at steady-state than these extreme examples. In the latter cases, and within the same forest type and therefore with the same litter quality, warmer and moister sites are likely to have *both* greater rates of turnover and higher productivity. Although a positive relationship exists, direct cause-and-effect between turnover and productivity is difficult to establish. Among forest types, differences in rates of forest floor turnover are related to differences in litter quality and in environment, and any relationships between productivity and turnover are even further removed from direct cause-and-effect.

Storage

The role of the forest floor in storing nutrients or water is often over-rated because the forest floor is physically obvious. Published ecosystem nutrient budgets must be carefully evaluated because most report the extractable or available forms of nutrients in mineral soil but include the *total* nutrients in forest floor, disproportionately weighting the importance of the latter. With comparable analytical techniques and because of its generally low bulk density, forest floor is usually a minor nutrient storage component. Forest floor has a similar minor role in storing water because of both its low bulk density and its large proportion of macropores. For example, forest floor water storage in white pine (*Pinus strobus* L.) stands in the north-eastern United States was about 1 cm, or about 10% of that of the underlying mineral soil (Mader & Lull 1968). Storage was defined as the difference between maximum water content following free drainage and minimum after extended dry periods. The roles of the forest floor as a mulch (i.e., in reducing surface evaporation) and in increasing water infiltration, reducing surface run-off, and hence reducing surface erosion, probably exceed its importance as a storage compartment in the hydrologic cycle.

EMPIRICAL RELATIONSHIPS

Many empirical approaches have attempted to quantify the link between soil properties, including SOM, and site quality (Coile 1952; Ralston 1964; Carmean 1975; Hagglund 1981). The major empirical approaches for assessing site quality are (1) *soil-site studies*, (2) the *decision-tree approach*, and (3) the *productivity index* (PI). The relationships that are reported are often blurred because the soil and associated site properties interact under the constraints imposed by both biology and climate, and because of imperfect measures of site quality (Monserud 1990; Berguson *et al.* 1994). As Ralston (1964) stated, probably facetiously, "Thus, analysis of environmental factors related to site quality need not be all-inclusive but merely sufficiently detailed to include all the important variables and sufficiently astute not to overlook any of them" (Ralston 1964, p. 179). In most cases, the empirical approaches have observationally related tree growth to SOM or to closely associated soil properties.

Soil-site studies rely on multiple regression to relate a measure of tree growth, usually site index, to soil and site properties (Jones 1969). Although used for decades (first by Haig in 1929) and giving rise to nearly 200 published reports (Carmean 1975), initial enthusiasm for soil-site studies was followed by questions about their soundness (Stone 1978). Because of their underlying empiricism the myriad studies have not identified a universal set of soil variables that are related to tree growth, but some variables have been common across species, landscapes, and geographic areas. The thickness of the surface mineral soil horizon, which is typically high in SOM, is frequently positively related to tree growth (Ralston 1964; Carmean 1975), as is the organic matter concentration of that horizon (Coile 1952). The relationship is often curvilinear, with small increases in SOM at low levels resulting in large increases in site quality (Carmean 1975). This is illustrated by data from over 300 pine and spruce plantations in Wisconsin (Wilde 1970). An absolute increase of 1% in SOM, equivalent to a doubling for the average jack pine (*Pinus banksiana* Lamb.) plantation, increased site index nearly 20% (Fig. 4) while a similar increase in SOM for the average white spruce (*Picea glauca* Moench (Voss)) plantation increased it by 20% and increased site index by 7% (Fig. 4). The results of soil-site studies suggest the importance of SOM to forest productivity.

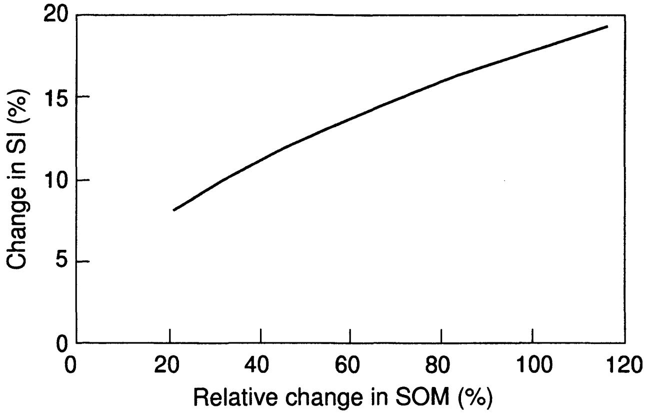

FIG. 4—Relative change in site index (SI) of conifer plantations (as percentage increase from initial value) with increase in SOM of 1% dry weight. Increase in SOM expressed as relative change from initial value. Based on data from about 320 pine and spruce plantations located on well-drained soils in Wisconsin, USA (Wilde 1970).

The decision-tree approach for assessing site quality uses an expert system procedure to identify and weight a set of soil properties that are important to site productivity. Initially developed for southern hardwoods (Baker & Broadfoot 1977, 1979), the same relationships were successfully applied to loblolly pine (Guldin *et al.* 1988). Modifications of properties and weightings have been applied to red alder (*Alnus rubra* Bong.) (Harrington 1986) and to both loblolly (Harrington 1991) and longleaf pine (*Pinus palustris* Mill.) (Harrington 1990). All applications use both SOM and related properties as important soil variables. For example, about one-third of the potential maximum site index of sycamore (*Platanus occidentalis* L.) is influenced by thickness of the A horizon, its SOM concentration, and its related properties of structure and bulk density (Baker & Broadfoot 1979).

In the third empirical approach, the PI, soil properties that limit or restrict tree root distribution from an assumed ideal are assumed to reduce the potential productivity of a site (Henderson *et al.* 1990). The limitations are quantified by sufficiency relationships, with a sufficiency rating of 1.0 representing the optimum level of a soil property for root growth and a rating of 0.0 representing an absolutely limiting level. Sufficiencies are evaluated by soil horizon or depth increment, and then accumulated to yield a PI with a maximum value of 1.0. The PI was developed for agronomy (Kiniry *et al.* 1983) and has been used there to evaluate productivity changes associated with erosion (Larson *et al.* 1983; Pierce *et al.* 1983). The major application of PI to forest soils has been by Gale and co-workers in the Great Lakes' states (Gale & Grigal 1988, 1990; Gale *et al.* 1991). The sufficiency relationships usually include properties closely related to SOM. For example, root growth is limited by increases in bulk density and by decreases in available water (Fig. 5), both related to SOM.

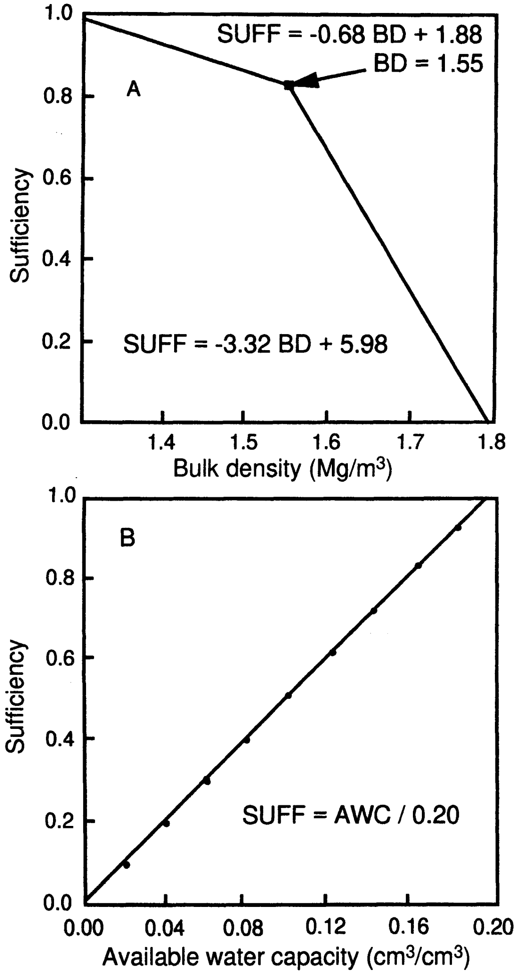

FIG. 5–Sufficiency (SUFF) of soil bulk density (BD) and available water (AW) for root growth as used in the original PI model (Kiniry *et al.* 1983) (from Henderson *et al.* 1990). A sufficiency rating of 1.0 represents the optimum level of a soil property for root growth and a rating of 0.0 represents an absolutely limiting level.

All of the empirical approaches would rate mineral soils with deep surface horizons that are high in SOM as more productive than soils with lower SOM. The former soils are likely to have high available water storage capacity, low bulk density, and high available nutrients. Unambiguous relationships between SOM and productivity are seldom demonstrated by these approaches, however, because of their empiricism and because of the covariation among soil properties. Although evidence of the importance of SOM to productivity based on these empirical approaches is circumstantial, that evidence is persuasive.

ORGANIC MATTER REMOVALS

Observations

Manipulations of SOM would appear to provide ideal assessments of its effects on forest productivity. Some of these manipulations are planned and others unplanned. Soil organic matter was inadvertently manipulated in Europe where litter was traditionally removed from forest stands to use as animal bedding, resulting in many examples of deleterious effects on productivity as first reported by Ebermayer in the late nineteenth century (Baule & Fricker 1970). On good sites, annual litter removal for two to three decades reduced stand annual increment by about 20% (Baule & Fricker 1970). Litter removal led to declines in SOM (15%) but proportionally even larger decreases in total nitrogen (25%) (Baule & Fricker 1970). Similarly, in every eight pairs of matched sites in Germany, productivity class was reduced on the member of the pair where litter had historically been removed (Wiedemann 1935). Sites were on coarse soil materials, and differed only in management due to ownership boundaries. Continued litter removal at other locations led to a drop of about 50% in SOM in the surface mineral soil and more than a doubling of resistance to penetration (soil strength) (Wiedemann 1935). The pertinence of these observations to forest management is simultaneously clear and confusing. Although they clearly indicate that SOM is important to forest productivity, the direct causal mechanism for the loss of productivity, whether due to altered nutrients, water, or soil physical properties, is uncertain.

Site preparation operations such as windrowing and scalping may inadvertently remove SOM. Their effects on productivity are difficult to evaluate because the absence of competition, one goal of site preparation, often provides short-term benefits to seedling growth. Following an extensive review of the literature, Morris & Miller (1994) concluded that "... long-term productivity is frequently deleteriously affected by mechanical slash removal such as windrowing but not by chopping or other operations that leave the majority of slash in place". Further review seems unlikely to change that conclusion.

Experiments

A dramatic example of the consequences of experimental litter removal was reported by van Goor & Tiemens (1963). Eight years after litter removal from six Scots pine (*Pinus sylvestris* L.) plantations (about 45 years old), volume increment decreased by about 30%. In another study, experimental removal of logging and thinning debris and continuing removal of annual litterfall in a second-rotation radiata pine plantation on a rhyolitic pumice soil in New Zealand produced a relatively small (12%) volume reduction after both 16 (Ballard & Will 1981) and 26 years (Dyck & Skinner 1990). The most significant effect was on soil properties at 5–10 and 10–20 cm depth, where by age 26 extractable calcium and magnesium had decreased by 69% and 66%, respectively (Dyck & Skinner 1990). Foliar analysis showed that "... B concentrations had been reduced to a level that was critical for radiata pine growth, Mg and N were marginal and Ca concentrations were barely adequate ..." (Dyck & Skinner 1990). Although rates of nitrogen mineralisation had apparently been maintained on the experimental plot, it was at a cost of soil capital (Ballard & Will 1981). The relatively small loss in productivity was attributed to the inherent fertility of the soils (Ballard & Will 1981), but the decreases in soil nutrient capital were expected to have negative implications for productivity of subsequent rotations.

The multiple roles of SOM in productivity are demonstrated by the effects of the removal of pine straw, the L or Oi forest floor horizon, from longleaf pine stands. Growth declines following straw removal in South Carolina (McLeod *et al.* 1979) were linked to water stress; xylem pressure potential increased with degree of removal with no significant nutritional effects noted in either soils or trees (Ginter *et al.* 1979). In contrast, decreases in productivity following straw removal in Louisiana were offset by nitrogen and phosphorus fertiliser application (Haywood *et al.* 1995). These seemingly contradictory results again demonstrate the multiple roles of SOM in maintaining both tree water status and nutrition.

Summary

Removal of SOM affects both the nutrient and water status of the forest system, and either or both may be the cause of reported declines in productivity. The impact of SOM removals is influenced by both the initial reserves of the system and the duration and magnitude of removals, with greatest relative impacts on sites with low inherent site resources (e.g., van Goor & Tiemens 1963; Wiedemann 1935). Specifically addressing nutrients, Dyck & Skinner (1990) identified sites most susceptible to productivity decline as those which "... have a large proportion of the labile pool of site nutrients contained in above-ground biomass and the forest floor." A similar statement could be made about sites where SOM makes major contributions to soil water status or physical properties.

ORGANIC MATTER ADDITIONS

Effects on Soil Properties

Another approach for evaluating the importance of SOM to forest productivity is to investigate sites where organic amendments, such as municipal and industrial biosolids, have been added. Although effects on soil nutrients depend on the type of material, effects on soil physical properties can be more broadly generalised. Most organic amendments increase soil aggregation and stability, reduce bulk density, and increase water-holding capacity and retention (Metzger & Yaron 1987; Tester 1990; Hill & James 1995). Increases in aggregate stability result from (1) the interaction between organic polymers in the biosolids and soil mineral components and (2) the stimulation of soil microflora (Metzger & Yaron 1987). Reductions in soil bulk density have been attributed to (1) the lower density of the added organic material and (2) increased soil aggregation and porosity (Hill & James 1995). In a variety of short- and long-term studies across a wide range of soil types, there was a positive linear relationship between increases in SOM and decreases in bulk density following additions of amendments (Khaleel *et al.* 1981). For the same range of soil types, 80% of the variation in water-holding capacity at field capacity and wilting point could be explained by sand content and change in SOM. Land-applied biosolids increase water retention, and a strong relationship between SOM and available water has been demonstrated in amended soils of contrasting texture despite significant differences in decomposition rates of the amendments (Fig. 6).

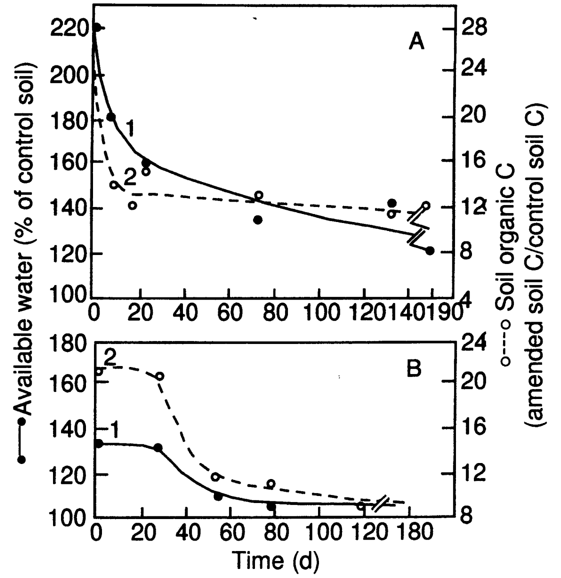

FIG. 6—Changes in available water (curve 1) and organic C content (curve 2) in (A) a sandy soil-undigested sludge (5%) mixture (Metzger 1986) and (B) a silt loam-digested sludge (5%) mixture (Epstein 1975) (from Metzger & Yaron 1987). Because of the high rate of addition of a high C material to a mineral soil with low C, increases in soil C were large.

Forest Responses

Despite measured changes in soil properties, directly ascertaining the influence of SOM on forest productivity from studies of organic amendments can be difficult because of confounding factors including (a) direct nutrient additions from the material, (b) changes in soil nutrient retention and availability, (c) changes in soil physical properties related to soil water, aeration, and temperature, and (d) changes in secondary factors such as weed competition. This multiplicity of potential effects results in forest responses that are often unique to the particular amendment and management regime and are difficult to extrapolate. Direct and indirect effects of added nutrients are particularly apparent with municipal and sewage biosolids, the most common organic amendments used in forested systems. In general, their application positively affects forest productivity (Brockway 1983; Harris *et al.* 1984; Henry 1986; Couillard & Grenier 1989; Hart & Nguyen 1994; Henry *et al.* 1994). Although increased SOM undoubtedly improves soil physical properties in many of these studies, the effect of added nutrients, especially nitrogen, is most often cited as the dominant factor affecting forest growth. Although concentrations can vary widely, these biosolids are typically high in nutrients, averaging about 3% N and 1.4% P (Hue 1995). On some sites, application of such biosolids can induce magnesium deficiencies (Harrison *et al.* 1996).

The most common industrial organic byproducts applied to forests are papermill wastewater treatment residuals, usually much lower in nutrients than municipal biosolids. Primary treatment residuals, produced in the largest quantities, often have C:N ratios of 100:1 to 200:1, which may result in nitrogen deficiencies (Camberato *et al.* 1997). Secondary treatment residuals are produced in smaller quantities, and because nutrients have been added for biological treatment they have higher nitrogen and phosphorus than do primary residuals. Nutrient availability is a key issue affecting forest response to papermill wastewater treatment residuals, with negative correlations between growth responses and the C:N ratio of the material (Henry 1986; Harrison *et al.* 1996). For example, on a sandy outwash soil low in SOM, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedling height responses ranged from a 146% increase on plots treated with secondary residuals to a 32% decrease on plots treated with primary residuals, with similar but less dramatic effects on the growth of noble fir (*Abies procera* Rehder) and western white pine (*Pinus monticola* D. Don) (Harrison *et al.* 1996). The primary factor affecting seedling growth thus appeared to be added nutrients rather than changes in soil physical properties.

On a fertile alluvial site in Oregon, primary treatment residuals with a C:N ratio over 200 increased initial cottonwood (*Populus deltoides* Bartr.) height growth 41% above that in control plots with fertiliser, and even greater increases (68%) occurred with a higher nutrient, primary/secondary treatment residual mix (Shields *et al.* 1986). After 3 years, increases in height growth were 31% and 38% for the primary and mixed treatment residual applications, respectively. At this site, growth was apparently limited by soil factors other than nutrients, but factors positively related to SOM. On a high-quality site in the south-east, sweetgum (*Liquidambar styraciflua* L.) growth also responded more positively to sewage biosolids than to inorganic fertiliser (Marx *et al.* 1995). Other studies have also shown positive tree responses to nutrient-enriched primary treatment residuals (Brockway 1983).

Although forest responses to land-applied biosolids and inorganic fertilisers have been directly compared, interpretations are difficult because a large fraction of nutrients in inorganic fertilisers is typically available to plants during the year of application whereas a significant portion of organically-bound nutrients in land-applied biosolids may take several years to mineralise. Municipal and industrial biosolids can also stimulate weed competition and alter understorey species composition (Brockway 1983; Harris *et al.* 1984; Henry 1986; Shields *et al.* 1986; Hart & Nguyen 1994; Henry *et al.* 1994), further confounding the effects of the organic matter on tree responses. Nutrient availability and retention were believed to be the key factors affecting productivity of jack pine and western red cedar (*Thuja plicata* D. Don) stands treated with various organic amendments and inorganic fertilisers (Weetman *et al.* 1995; Prescott & Zabek 1997). A single addition of straw stimulated growth of a jack pine stand in Quebec to the same extent as repeated fertiliser-nitrogen additions, with positive effects lasting 11 years (Weetman *et al.* 1995) despite the fact that the total nitrogen added in the straw (130 kg/ha) was much less than that added by the fertiliser (336 kg N/ha). Positive effects of the straw were attributed to increased nitrogen retention and to reduced competition from ericaceous vegetation. Straw additions also increased productivity of a western red cedar plantation in British Columbia more than either fish-wood compost or previous inorganic fertiliser or sewage biosolid treatments (Prescott & Zabek 1997). The investigators concluded that, despite similar levels of nitrogen, the straw sustained higher nitrogen availability for a longer time than did the compost or biosolids because it provided more readily available carbon for microbial activity.

To distinguish confounding factors associated with land-applied biosolids, studies that evaluate (1) long-term changes in SOM, nutrients and other soil properties, and productivity following application, and (2) effects of biosolid applications to disturbed or impoverished sites should both be useful. Harrison *et al.* (1995) identified potential trends in soil nutrients following application of organic amendments as (i) an increase above the level of application due to enhanced productivity of vegetation and/or internal retention, (ii) a permanent increase at the amended level, (iii) a gradual loss to the original level, or (iv) a loss beyond that added due to secondary effects such as enhanced decomposition of native SOM (Fig. 7). Most sites examined in the Pacific Northwest fell somewhere between (ii) and (iii) (Harrison *et al.* 1995). These same trend lines also apply to potential changes in SOM. Trends in nutrients and SOM reflect the balance of processes related to decomposition, mineralisation, and immobilisation, and the response of vegetation and its return of organic matter to the soil via above- and below-ground litter. Comparisons of trends in SOM with those in nutrients could help reveal mechanisms underlying tree growth responses.

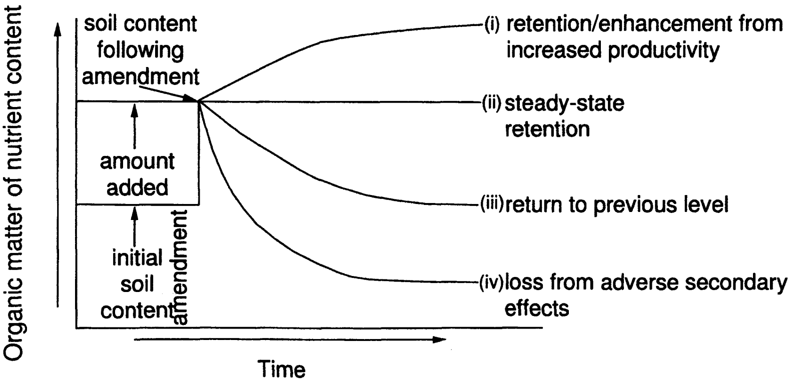

FIG. 7–Potential trends in soil organic matter and nutrients following application of organic amendments (from Harrison *et al.* 1995).

On mine reclamation sites, organic amendments such as wood chips, sawdust, sewage biosolids, and papermill wastewater treatment residuals generally increase and sustain productivity of trees and forage to a greater extent than do inorganic fertilisers (Roberts *et al.* 1988; Schuman & Belden 1991; Schoenholtz *et al.* 1992; Feagley *et al.* 1994). On these and other degraded sites, there are also overwhelmingly positive effects of organic amendments on soil properties such as water availability and retention, aggregation, and nutrient retention. Studies in the south-eastern United States of degraded borrow pits amended with biosolids provide solid evidence of the importance of SOM to forest productivity (Marx *et al.* 1995). In one South Carolina study, survival and growth of planted loblolly pine seedlings were very poor at a borrow pit with heavy clay Ultisols. Three years after application of sewage biosolids, however, pine seedling volume growth was 28 times greater on biosolids plots than on plots to which fertiliser and lime were applied, despite increased herbaceous competition on the biosolids plots. After 10 years, seedling performance was still dramatically higher on biosolids plots and the differences continued to increase over 18 years of measurement. Biosolids plots also contained nearly three times higher CEC and SOM in the upper 20 cm of soil than those receiving fertiliser and lime. Interpretations from the study were complicated, however, by differing nutrient additions with biosolids (34 Mg dry wt/ha, containing about 680 kg N/ha and 340 kg P/ha) and fertiliser (about 56 kg N/ha, 22 kg P/ha). In a second study on a borrow pit of compacted deep clay, one-half as much biosolids and twice as much fertiliser and lime as in the previous experiment were applied. After 7 years, loblolly pine seedlings on the biosolids plots had four times greater volume growth than those on fertiliser plus lime plots, and at age 14 volume growth was five to six times greater (Marx *et al.* 1995).

In summary, positive effects of organic amendments on soil properties and forest growth have been widely documented but the specific factors responsible can be difficult to isolate. The benefits of all types of biosolids on soil physical properties have been clearly demonstrated, particularly on degraded soils. Differences in growth responses to biosolids high in nutrients compared to those with high C:nutrient ratios illustrate the importance of nutrient concentrations and availability on response. Secondary effects associated with applications, such as weed competition, have also frustrated efforts to separate cause and effect. Despite these difficulties, studies of organic amendments have demonstrated positive effects of SOM on productivity. Longer-term factorial field experiments that isolate particular factors being supplied by organic amendments across a wider range of forest and soil types should help clarify relationships.

SANDY SOILS — A SPECIAL CASE

Studies on sandy soils should provide the clearest examples of the direct effects of SOM on forest productivity because the mineral fraction of such soils lacks significant water- or nutrient-retaining capability; those properties are nearly wholly a function of SOM. As an example, 25 forest stands on sandy soils in The Netherlands that had been deeply tilled 50 to 100 years before (for weed control following a Scots pine harvest) were compared with 25 similar untilled stands (van Goor 1952). Results showed that the tillage led to a 30% loss in SOM and nitrogen, a 50% loss in phosphorus, a reduction in aggregate stability, and a 25% decrease in field capacity (van Goor 1952).

Retention of logging residues (slash) had positive effects on productivity of sandy soils in the Mt Gambier region of Australia. Growth of second-rotation *Pinus radiata* plantations (2R) was compared to historical data from first-rotation plantations (1R) on the same sites and to first-rotation plantations established on carefully matched nearby sites with native vegetation (Flinn *et al.* 1980; Squire *et al.* 1985; Farrell *et al.* 1986). In contrast to the more common practice of burning, slash was retained when the 2R stands were established. At five years, growth on low-quality 2R sites (30 m^3/ha) was about five times greater than that recorded in the original 1R or that measured on the matched sites (Squire *et al.* 1985). The results were attributed to improved water and nitrogen status on the 2R sites due to the mulching effect of the litter and slash. Further study (Farrell 1984; Farrell *et al.* 1986) showed that improved soil water status was also related to suppression of weeds by the residues. In the same region, combinations of slash retention with fertiliser and weedicide treatments significantly improved growth of *P. radiata* at 15 years (Hopmans *et al.* 1993). A contradictory lack of significant effects of slash retention on *P. radiata* establishment (Smethurst & Nambiar 1990) was attributed to the fact that those treatments provided optimal nutritional conditions and complete weed control (Hopmans *et al.* 1993). These studies demonstrated that retained residues may have multiple positive effects at plantation establishment, and that careful (and costly) husbandry can provide surrogates for most or all of those effects.

Residues can also affect nutrient retention. In very sandy soils in New Zealand, Smith *et al.* (1994a) concluded that nitrogen leaching in the first 2–3 years after harvest of a 42-year-old 1R *Pinus radiata* stand indicated an inability of the system to retain nitrogen. When slash was retained at the site, nitrogen retention substantially increased, probably as a result of microbial immobilisation in residues with high C:N ratios. Continuing nitrogen immobilisation 5 years after harvest may have slightly reduced productivity, however (Smith *et al.* 1994b). Although most attention with respect to nutritional effects of SOM is on nitrogen status (Carlyle 1994), there is also a strong linkage between those properties and phosphorus in sandy soils. In the Mt Gambier region, potential nitrogen mineralisation was strongly related to organic phosphorus ($r^2 = 0.70$) but not to total nitrogen (Carlyle *et al.* 1990). In many very sandy soils, nearly all stored phosphorus is organic because there are only traces of the iron and aluminium compounds that usually retain phosphorus. This was demonstrated in the maritime coastal dune region of New Zealand, where virtually all phosphorus in the forest floor and surface mineral soil was organic, with about half being microbial phosphorus (Parfitt *et al.* 1994). Because phosphorus was not retained by these systems, 50% (of 125 kg/ha after 7 years) to 75% (of 100 kg/ha after 11 years) of added phosphorus fertiliser was lost by leaching. Soil OM is therefore essential for retaining nutrients in sandy soils.

Even in sandy soils, SOM is important in enhancing soil resistance to disturbance. Although sandy soils are usually considered to be relatively resistant to compaction (Lewis 1991), their degree of compaction is negatively related to SOM and positively related to soil water content at the time a load is applied (Sands *et al.* 1979). Sandy soils can show sharp increases in soil strength with small increases in bulk density (Sands *et al.* 1979), and such increases in strength and penetration resistance can exceed levels that reduce tree rooting (Greacen & Sands 1980). In the study in the Mt Gambier region (Flinn *et al.* 1980; Squire *et al.* 1985; Farrell *et al.* 1986), the degree to which growth on the 2R sites exceeded that on the 1R sites was much less on high-quality than on low-quality sites. This was attributed in part to deleterious alteration of soil physical properties associated with intermediate thinnings that were carried out during the first rotation on the high-quality sites but not on the lower quality sites (Squire *et al.* 1985). Higher levels of SOM can mitigate effects of management activities on compaction and soil strength.

Although studies on sandy soils provide a link between SOM and forest productivity, they also illustrate complex interactions, feedbacks, and unexplained variation. Nonetheless, the strong weight of evidence indicates that residue retention on sandy soils enhances plantation establishment, retains essential nutrients, and helps maintain soil physical properties. Sands (1983, p. 146) concluded that "... the most important single factor in the long-term maintenance of productivity on these soils [of the Mt Gambier region] is maintenance of soil organic matter."

IMPLICATIONS FOR FOREST MANAGEMENT

Over-riding Constraints

The weight of evidence reported in this review, much of it circumstantial, indicates that SOM and forest productivity are positively related. Further, forest management operations can influence levels of SOM (Johnson 1992a). Productivity:SOM relationships are complex in forests, however, because of the dramatic effects of climate, forest type, and other soil properties on both productivity and SOM dynamics. These effects strongly determine or constrain the role of SOM in influencing forest productivity and the ability of forest managers to manipulate SOM. Globally, forest productivity generally increases with increasing temperature and precipitation (Fig. 8), and the most productive systems tend to have the lowest soil carbon (Fig. 9). Similarly, over a range of temperate forest sites, productivity as measured by litterfall increased with mean annual temperature while organic matter in both forest floor and mineral soil concurrently decreased (Johnson 1995). These contrasting trends are caused by two opposing forces; more productive forests produce more biomass and organic inputs to the soil, but they exist and produce litter in climates that favour rapid decomposition rates. Vogt *et al.* (1986) reported that deciduous forests had only 50% of the forest floor mass of evergreen forests below latitude 40°, increasing to 75% at higher latitudes. They concluded that climatic factors were significant for litterfall production but that differences in forest floor mass within climatic zones were likely due to differences in litter quality that affected decomposition and accumulation.

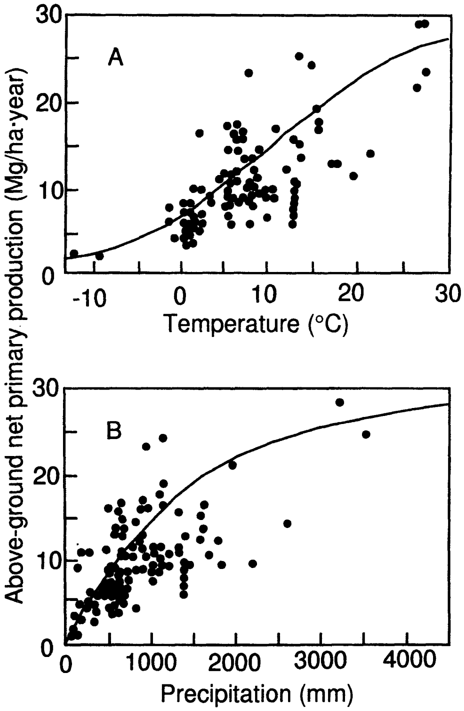

FIG. 8—General trends of increasing forest productivity with increasing temperature and precipitation (from O'Neill & DeAngelis 1981).

This conclusion can also be illustrated by relationships with actual evapotranspiration (AET), a measure that integrates temperature and precipitation and is frequently used as a surrogate for heat and water availability. Globally, forest production as measured by litterfall has a strong positive relationship with AET (Meentemeyer *et al.* 1982), as does the rate of

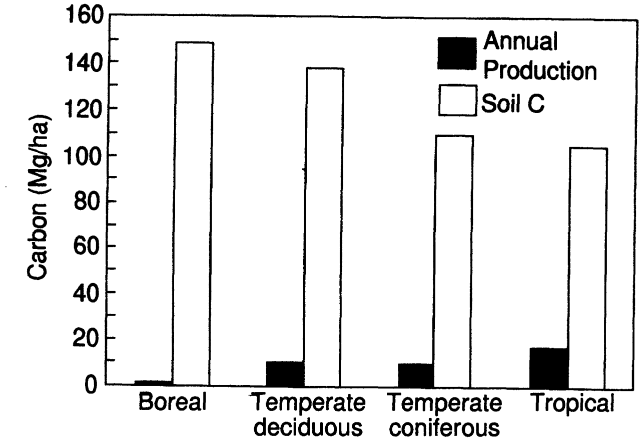

FIG. 9—Annual above-ground production and soil carbon of major forest ecosystems. Data from Van Cleve & Powers (1995).

litter decomposition (Meentemeyer 1978). Decomposition is also, however, negatively related to litter quality as measured by lignin concentration (Meentemeyer 1978). Over a range of temperate forest sites, the steady-state decomposition ratio, *k* (Olson 1963), increased with temperature but was lower for conifers (Johnson 1995). Consistent with these trends, forest floor mass varies with forest type and is negatively related to AET within types in the Great Lakes' states (Grigal & Ohmann 1992) and in Europe, where climate is approximated by latitude rather than AET (Gärdenäs 1998). Properties of the soil also affect SOM, the most obvious being a positive relationship with clay content (Great Lakes' states — Grigal & Ohmann 1992; Pacific Northwest — Homann *et al.* 1995).

Within climatic zones, and even within forest types, tree growth rates may directly and indirectly affect forest floor accumulation rate. Although species with higher growth rates may produce more litter than slower-growing species, they also generally have high rates of carbon and nutrient cycling (Schulze & Chapin 1987). This is due, in part, to higher tissue concentrations of nutrients, lower concentrations of cell wall components (e.g., lignin), and lower concentrations of secondary compounds that inhibit microbial activity (Lambers & Poorter 1992). Water or nutrient stress can also increase secondary compounds in plant tissue and reduce its quality for microbial decomposers (Lambers & Poorter 1992). Productivity:SOM relationships also change as forests age (Gower *et al.* 1996; Ryan *et al.* 1997). In particular, the ratio of leaf:woody detritus decreases, slowing decomposition rates due to the higher lignin content and lower woody litter surface area:volume ratios. Litter quality also decreases with age due to decreased nitrogen uptake by vegetation and retranslocation of nitrogen from senescing foliage to living, woody biomass. A positive feedback occurs as litter quality declines, SOM accumulates, nutrients are immobilised, and biomass allocation shifts from above-ground tissues to fine roots and mycorrhizas.

Management Strategies

Where does this discussion lead? In answer to the question posed in the **Introduction**, there does not appear to be a *direct* link between SOM and forest productivity. Apparent relationships are based on other soil properties that are influenced by SOM and influence productivity. Even in sandy soils, or with experimental organic removals or additions, links between SOM and productivity are obscured because of multiple interactions. In nearly every reported case, the effect of SOM on productivity is related to a soil chemical or physical property that is related in some way to SOM. These latter relationships are not absolute, but instead are associated with other covarying soil properties. In the absence of direct proof, circumstantial evidence must be accepted as adequate. The importance of SOM in sustaining plant productivity in managed systems is probably most clearly demonstrated in agriculture. This is particularly evident on coarse-textured soils where practices that increase organic matter can have dramatic effects on water conservation, nutrient availability, root penetration resistance, and crop yield (Tester 1990; Rasmussen & Collins 1991).

Long-term data from forests are difficult to obtain, but there are numerous examples showing detrimental effects on productivity due to losses of organic matter associated with management. Although effects of site preparation were discussed earlier, an example will illustrate the point. A rotation-length chronosequence for loblolly pine indicated that removing organic residues prompted an early positive growth response that declined precipitously by age 10, thereafter resulting in less volume than the controls (Fig. 10) (Powers *et al.* 1994). The conclusions were considered to be tentative because of potential site differences and secondary effects of site preparation (Powers *et al.* 1994). However, these data, in concert with those summarised by Powers (1991) and Morris & Miller (1994), further demonstrate the importance of SOM to stand productivity. Johnson's review (Johnson 1992a) indicated that many forest management activities have minor effects on soil carbon (i.e., SOM), but that in some situations SOM is clearly increased or reduced by management. For example, referring to site preparation practices for radiata pine in New Zealand, Balneaves (1990) stated that "The build-up of slash and litter has taken 30 years of a forest crop to establish and any beneficial effects from this can be negated within a 4-hour (per hectare) operation". Conversely, Johnson's review (1992a) clearly showed that fertiliser application can increase SOM and that residue inputs from some harvesting activities can substantially increase SOM. Important questions also remain about relative contributions of above- and below-ground material to SOM.

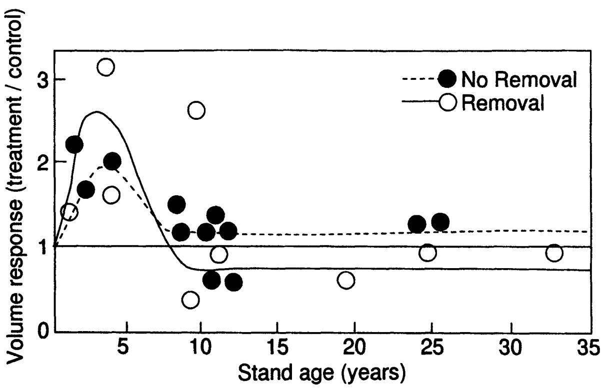

FIG. 10–A chronosequence of volume response of loblolly pine to removal of organic residues by site preparation (from Powers *et al.* 1994; data reviewed by Burger & Kluender 1982).

Because of the myriad interactions of SOM with soil chemical and physical properties, it is unlikely that any experimental approach can clearly demonstrate the direct influence of SOM on productivity. Despite the difficulty, there are some experimental approaches that could further clarify relationships. Firstly, long-term studies are needed where specific sites are followed through time. Long-term studies are not synonymous with large investments. Instead, good site histories and a basic set of periodic measurements collected from a number of sites would provide much more meaningful information than a detailed set of measures collected over a short time period. Sites should be classified into groups based on fundamental similarities, including physical features and level of management. Both responses to treatments within the groups and differences in response among groups should be tested. There undoubtedly will be significant inter-site variation in response. However, the primary goal should be identification of general trends over classes or groups of sites; the statistical equivalent of blocking can accommodate that variation. Before treatments are selected, the systems must be understood, and especially the primary limitations to forest productivity and the potential role of SOM in compensating for or mitigating those limitations. Treatments, then, should be cognisant of the covariation among soil properties and focus on correcting those limitations with and without SOM.

Secondly, additional chronosequence studies provide an opportunity for near-term answers to specific questions. In many cases, forest scientists and managers simply do not have the luxury of waiting for results from long-term experiments to unfold. A major challenge with this approach is the variation in soil and site characteristics that is not related to SOM or to the properties of interest. As with other types of field studies, the validity of the information provided by chronosequence investigations strongly depends on the quality of available site data and land use histories. More work is needed to identify potential sites and databases that have been overlooked. In other cases, new perspectives or additional measurements can uncover valuable information for even well-documented studies. Companion experiments in which specific factors of interest are controlled can also be useful in interpreting results from chronosequence studies.

Finally, models have the potential to quantitatively and succinctly summarise the complex interactions of SOM and forest management, including differences in systems' response because of differences in initial conditions. Models provide the opportunity to assess the effects of a variety of operations that are well beyond those that can be implemented on-the-ground because of time and cost constraints. For example, Morris *et al.* (1997) assessed the effects of two different rotation lengths (40 and 80 years) and levels of utilisation (tree-length and whole-tree) on simulated Douglas-fir forests that were previously unmanaged or degraded by organic matter loss. Based on a simulated 240-year period, they concluded that intensive management (40-year rotation and whole-tree harvest) of a previously unmanaged forest would lead to a rapid drop in SOM with associated nutrient deficiencies. In contrast, less-demanding management regimes allow previously degraded sites to recover. Similar long-term experiments are simply impossible to carry out in the field.

Models, however, are not a panacea. Results of simulations are a function of a myriad of incorporated assumptions, many untested and some unstated. Even state-of-the-art models whose focus is SOM, such as CENTURY (Parton *et al.* 1993), are hampered by our lack of understanding of ecosystem processes that occur after forest management operations.

Models that deal primarily with forest growth-and-yield usually trivialise or even ignore the influence of management on SOM. Those models that attempt to directly address the relevant issues are usually constructed and calibrated within a single geographic area with one or a small set of forest types, and they lack validation if applied to other areas. Many of the issues that must be considered in evaluating SOM models are similar to those necessary to evaluate models that simulate effects of climate change on forests (Loehle & LeBlanc 1996). These caveats, however, are not meant to denigrate the use of models. The results of any simulation must simply be interpreted critically, with assumptions made explicit, and at best those results may simply suggest issues of concern.

Initial SOM levels and soil texture are two key characteristics that affect the response of a soil to additions or losses of SOM. Management practices that add or remove organic matter will have the greatest effect on sites with low initial SOM levels, because of more significant changes in nutrient supply and water relations. Many sites with coarse-textured soils are naturally low in SOM and are also susceptible to SOM losses because of their low clay content, which may protect SOM from rapid microbial decomposition. Such soils also tend to have low water- and nutrient-holding capacities that can be dramatically improved by increases in SOM. Fine-textured soils may respond positively to organic matter additions through improvements in structure and aeration. Because of the presence of clays, such soils tend to be naturally higher in SOM than coarse-textured soils and will also tend to retain added organic matter for longer periods of time. Consequently, additions of organic matter to such sites may have less dramatic initial effects than additions to coarse-textured soils but the effects are likely to be sustained over a longer period.

The conclusions of this review, and of many previous reviews (Sands 1983; Powers *et al.* 1990, 1994; Powers 1991; Johnson 1992a; Morris & Miller 1994; Henderson 1995; Jurgensen *et al.* 1997), can be schematically summarised (Fig. 11). SOM occupies a central position in affecting the major three classes of soil properties—physical, chemical, and biological (Fig. 11 A). The influence of SOM on productivity, however, is only indirect through its effect on the other properties and their direct effects on productivity (Fig. 11 B). Productivity, assessed by the amount of organic matter produced, directly affects SOM and through it affects the other soil properties (Fig. 11 B). Even the broad generalisations that are expressed in this Figure must be considered in two distinct groups because of the relative importance of organic matter in coarse- *versus* fine-textured soils. Changes in productivity with SOM are likely to be proportionally less on fine-textured soils, especially if poorly-drained, than on coarse-textured soils, especially if well- to excessively-drained. Another key point is that the effect of changes in SOM on productivity is directly related to the site and specifically to the pre-existing soil-based limitations to productivity at that site. Effects of changes in SOM on forest productivity will be manifested through their influence on factors that limit productivity. For example, if limitations are related to nitrogen availability, and if increases in SOM increase that availability, then effects will be positive. Similarly, SOM may enhance productivity where it helps increase aeration on a compacted soil. Management activities can directly affect soil properties, including SOM, and hence influence future productivity. The direction and degree of change of SOM by management have been the subject of many studies, and it is clear that responses are not the same over all sites, and that more work is needed to place the variation in response into a universal framework.

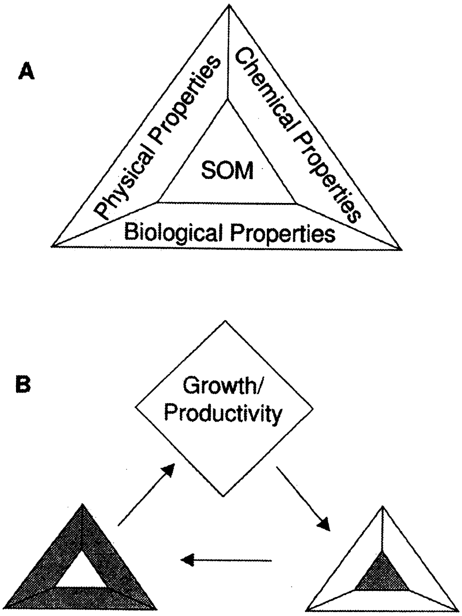

FIG. 11–Schematic illustration of the close inter-relationship among soil properties (A) and the inter-relationship of soil properties (shaded) and growth/productivity (B). Soil organic matter affects the major three classes of soil properties (A) but only indirectly affects productivity (B). Productivity directly affects SOM and through it affects the other soil properties, which, in turn, affect productivity (B).

CONCLUSIONS

The question of the influence of soil organic matter (SOM) on forest productivity is both simple and complex. The question is complex in the sense that the myriad interactions of SOM with soil chemical and physical properties make it unlikely that the direct influence of SOM on productivity can be clearly demonstrated. In addition, SOM is not an independent variable, but its levels in soil depend on plant productivity, the chemistry of the plant litter, and on environmental factors such as temperature and water. Thus SOM is inextricably linked to productivity and to those factors that influence it. The particular role and contribution of SOM to productivity vary greatly, however, depending on limiting environmental factors. In coarse-textured soils, SOM is clearly important for retaining water and for supplying and retaining nutrients. As soils become finer, with more silt and clay, the roles of SOM in nutrient and water become less important but its role in promoting soil physical properties that are conducive to root growth increases. The effects of management-induced changes in SOM on forest productivity also depend on the initial amount of SOM. Although inherent properties of the mineral soil may compensate for or mitigate the effects of SOM loss on some sites, the importance of SOM to long-term site productivity has been demonstrated across the full range of mineral soil textures. Because of the strong ties of SOM to a wide range of soil properties and functions, prudent forest management policies should consider the implications of practices on SOM, and in most cases should be designed to maintain or enhance SOM levels.

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