Forest floor microbial biomass across a northern hardwood successional sequence

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Abstract

Microbial dynamics partially control forest productivity, yet are poorly understood in the northern hardwood forest. Following forest cutting, microbial biomass may reflect changes in the forest floor environment. Using direct counts, forest floor microbial biomass was studied in a sequence of northern hardwood forest stands ranging in age since clearcutting from 3 to more than 120 yr. The organic horizon was collected 3 times in each of 1994 and 1995, in June, August and October. Samples were analyzed for active fungi, active bacteria, pH, forest floor moisture content and organic fraction. Forest floor temperature was measured in the field with each collection; forest floor mass was measured once in each stand. In 1995, forest floor samples were also analyzed for total N, nitrate and ammonium. Amounts of active microbial biomass (fungi plus bacteria) ranged from 38 to 103 μg g^{-1} organic matter; active microbial biomass per unit area ranged from 40 to 800 mg m^{-2} forest floor organic matter. Microbial biomass varied significantly among sampling periods in 1994, but not in 1995, and was greater in early- and late-successional stands than in mid-successional stands. Microbial biomass was not very responsive to the environmental factors measured in this study. Moisture content was the environmental variable that most often contributed to variation in microbial biomass, and together with additional factors explained only 23% of the variation in 1994, and only 27% in 1995. Lower microbial biomass in mid-successional stands suggests that microbial dynamics in this forest are not controlled by factors directly related to forest harvesting. © 1999 Elsevier Science Ltd. All rights reserved.

1. Introduction

The forest floor in the northern hardwood forest is important structurally and functionally. It serves as the rooting zone for up to 40% of the fine roots in lower montane forest stands (Fahey and Hughes, 1994), is a major storage component for ecosystem organic matter and nutrients (Gosz et al., 1976), and plays an important role in ecosystem recovery following disturbance (Marks and Bormann, 1972; Marks, 1974). Nutrients needed for forest growth and maintenance are bound in the forest litter and released through decomposition by microorganisms. Microbial mineralization and immobilization therefore affect nutrient availability and ultimately forest productivity (Parkinson, 1979; Zak et al., 1990).

Forest harvesting alters the amount of soil organic matter (Federer, 1984; Mattson and Smith, 1993), soil temperature, soil moisture and pH (Bormann and Likens, 1979), all of which affect microbial activity (Harvey et al., 1980; Hendrickson et al., 1985; Entry et al., 1986). Numerous studies have documented significant short-term responses of microbial communities to forest harvesting (Sundman et al., 1978; Bååth, 1980; Lundgren, 1982; Ingham et al., 1993). Microbial biomass dynamics during succession also have been studied (Insam and Haselwandter, 1989; Zak et al., 1990; Klein et al., 1995), but not following forest harvest. Despite the important functions of the forest floor in the northern hardwood forest, little is known about the long-term dynamics of microbial biomass following forest harvesting.

We examined forest floor microbial biomass using direct microscopic counts as part of a larger study examining forest floor properties in a chronosequence of northern hardwood forest stands harvested between

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3 and more than 120 yr ago. We used the direct microscopy method for quantifying microbial biomass because this method distinguishes fungi from bacteria, which can reveal shifts in their relative importance during succession (Ingham et al., 1993; Klein et al., 1995). The objectives of this study were (1) to quantify forest floor microbial biomass across a chronosequence of forest stands following harvesting and (2) to relate successional trends in microbial biomass to environmental factors known to control microbial biomass or to change with forest succession, such as forest floor C, soil moisture, soil temperature and pH. We hypothesized that forest floor microbial biomass would be responsive to forest floor moisture and organic matter content (Sundman et al., 1978; Entry et al., 1986). We expected that microbial biomass would be highest in early succession, reflecting changes in litter quality and nutrient availability as well as soil moisture and organic matter content.

2. Materials and methods

2.1. Site description

Forest floor microbial biomass was examined across 16 northern hardwood forest stands in the White Mountain National Forest in north-central New Hampshire in 1994 and 1995. One of our 16 stands was located at the Hubbard Brook Experimental Forest (HBEF); the other 15 stands were located between 80 and 130 km from HBEF. The stands were typical of lower montane zone forests in this region (Frye, 1980). The mature stands consisted primarily of American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britton); younger stands were dominated by pin cherry (*Prunus pensylvanica* L.). The soils of this area developed on granitic glacial till overlying granitic gneiss (Huntington et al., 1988). The soils of the sampled forest stands were well-drained to moderately well-drained Orthods with a mor-type forest floor (Federer, 1984). The climate of the north-central White Mountains is classified as cool–temperate humid continental with a mean temperature of −9°C in January and 19°C in July (Likens and Bormann, 1995). Average annual precipitation at HBEF is 130 cm, with approximately 30% falling as snow (Likens and Bormann, 1995).

In 1994 we measured microbial biomass in 13 stands in the White Mountain National Forest that had been used in a study of the forest floor (Federer, 1984). In 1994, these stands ranged in age from 10 to more than 120 yr since harvesting (Table 1). Six of the 13 stands were located in the Bartlett Experimental Forest, a 1052 ha forest located in the White Mountain National Forest. In 1995, the six stands located in the Bartlett Experimental Forest were resampled. In addition, three younger stands in the Bartlett Experimental Forest were located and sampled in 1995 to improve representation of early-successional stands (< 12 yr old). Thus, a total of 9 stands, ranging in age from 3 to more than 120 yr, were sampled in 1995 (Table 1).

A major assumption of this study is that stand age is an independent factor. Unfortunately, stand age is not independent of treatment; historic changes in logging practices could be an important variable, but one we cannot separate from stand age. In addition, although we endeavored to minimize the variation in site not attributable to stand age by selecting sites for their similarity, inherent site differences could contribute to differences in measured variables.

Prior to sampling in 1994, we relocated the 13 stands used by Federer (1984) which had been permanently marked. In 1995, we located and permanently marked three new stands, 3, 4 and 5 yr of age. Within each of the 16 stands, 5 transects were systematically positioned, all 50 m long, except in one stand from the previous study that was smaller than the rest. In this stand, transects were 33 m long.

2.2. Sample collection and laboratory analyses

Forest floor samples for quantification of microbial biomass were collected in June, August and October of 1994 and 1995. Twenty 2-cm dia cores were collected along each of the 5 transects per stand at evenly spaced intervals, with 2 cores per sampling location and 10 locations per transect. The forest floor was separated from the mineral horizon in the field based on visual characterization. The O_{ea} horizon was collected; the O_i (litter layer) was discarded. The cores were composited by transect for a total of 5 samples per stand. The samples were stored in ziplock bags and kept at 4°C until microbial analysis could be carried out, within a week of sample collection. Forest floor temperature was measured in the field at three systematically determined locations per transect in each plot.

Active fungal and bacterial biomass in forest floor samples were quantified using direct count epifluorescent microscopy (Ingham and Klein, 1984; Lodge and Ingham, 1991). Direct count estimates of microbial biomass were determined in a dilute 1:10 soil suspension stained with fluorescein diacetate (FDA). Active fungal hyphae (250×) and active bacteria (400×) were quantified on the same slide using epifluorescent microscopy. Active fungal and bacterial biomass were calculated from the volume of fungi or bacteria in 1 g of dry forest floor using estimates of hyphal and bacterial diameters and the assumption that hyphal tissue

Table 1
Successional status, age since harvesting, location of northern hardwood stands in the White Mountain National Forest, and dominant species of stands in this study. Except for the three youngest stands, the dominant species listed for each stand made up at least 75% of the stand basal area. For the three youngest stands, no basal area was recorded because there were no stems ≥2 cm dia; for these stands, dominant species were determined by stem density

Stand age	Location	Dominant Species[a]	
		2–10 cm dia	> 10 cm dia
Early succession			
3[b]	Bartlett Exp. Forest	AcSa, BePa, FaGr	
4[b]	Bartlett Exp. Forest	BePa, FaGr, PrPe	
5[b]	Bartlett Exp. Forest	BePa, FaGr, PrPe	
12[bc]	Bartlett Exp. Forest	BeAl, BePa, PrPe	
16[c]	Sabbaday Falls	BeAl, PrPe	AcSa, PrPe, TsCa
18[c]	Jackson	AcSa, FaGr, PrPe	BePa, PoGr
Mid succession			
25[c]	Hubbard Brook Exp. Forest	BeAl, PrPe	BeAl, PrPe
28[bc]	Bartlett Exp. Forest	BeAl, FaGr, PrPe	AcSa, BePa, PrPe
39[c]	Sawyer River	AcPe, BeAl, FaGr	AcSa, BeAl, FaGr
46[c]	Iron Mountain	AcPe, AcSa, FaGr	BeAl, BePa, FaGr, FrAm
49[c]	Iron Mountain	AcSa, FaGr	AcSa, BePa, FaGr, FrAm
55[bc]	Bartlett Exp. Forest	AcSa, FaGr	AcRu, AcSa, BePa
59[bc]	Bartlett Exp. Forest	AcSa, FaGr	AcRu, BeAl, BePa
Late succession			
85[c]	Jackson	FaGr, PiRu	AcRu, BeAl, FaGr
> 120[bc]	Bartlett Exp. Forest	AcSa, BeAl, FaGr	AcSa, FaGr, FrAm
> 120[bc]	Bartlett Exp. Forest	FaGr	AcRu, BePa, FaGr

[a] *Acer pensylvanicum* (AcPe); *A. rubrum* (AcRu); *A. saccharum* (AcSa); *Betula alleghaniensis* (BeAl); *B. papyrifera* (BePa); *Fagus grandifolia* (FaGr); *Fraxinus americana* (FrAm); *Populus grandidentata* (PoGr); *Picea rubens* (PiRu); *Prunus pensylvanica* (PrPe); *Tsuga canadensis* (TsCa).
[b] Stands sampled in 1995.
[c] Stands sampled in 1994.

density averages 410 mg cm^{-3} and bacterial tissue density averages 330 mg cm^{-3} (Ingham et al., 1991).

In 1995, forest floor samples were analyzed for NO_3^- and NH_4^+. Forest floor samples for inorganic N analysis were stored at 4°C for up to 2 d prior to KCl extraction. Extracted samples were filtered through No. 40 Whatman filter paper and the extract analyzed for NO_3^- and NH_4^+ using a Technicon Auto-analyzer II.

After removal of material for microbial analysis, forest floor samples were air-dried, ground and sieved to 2 mm and carefully divided to ensure representative subsamples. One gram of oven dried sample material was ashed (500°C) and reweighed for organic fraction determination. Soil pH was determined on air-dried samples using the calcium chloride method (Hendershot et al., 1993). Total N and total C were determined once in 1994 and once in 1995 on samples pooled across sampling dates. Samples were analyzed for total N and C by combustion, using a Leco CN Analyzer.

We report the amounts of fungal and bacterial biomass on an organic matter basis (μg microbial mass g^{-1} organic matter). These units are preferred to con-

centrations per unit mass because the mineral fraction of the forest floor contributes little to microbial activity but has a large influence on bulk density (Federer et al., 1993). Concentrations per unit mass would be quite sensitive to variations in organic fraction (organic mass per unit mass of soil). We also report microbial biomass per unit area, which is the product of microbial biomass concentrations per unit organic matter and the organic matter per unit area, obtained from quantitative surveys of these stands (unpublished).

2.3. Statistical analysis

Statistical analyses of the effects of stand age on measured forest floor variables were performed by grouping the stands into early, middle and late succession. The criteria used for grouping were species composition coupled with descriptions of northern hardwood forest successional patterns (Covington and Aber, 1980; Covington, 1981; Federer, 1984). Early-successional stands were those with a large pin cherry or *Rubus* sp. component, ranging in age from 3 to 18 yr since harvesting ($n = 3$ in 1994; $n = 4$ in 1995;

Table 1). Mid-successional stands were dominated by American beech, yellow birch, sugar maple and red maple with a small component of pin cherry in the younger stands, ranging in age from 25 to 60 yr since harvesting ($n = 7$ in 1994; $n = 3$ in 1995; Table 1). The late-successional stands were dominated by similar species as the mid-successional stands, with the exclusion of pin cherry, and ranged in age from 85 to more than 120 yr since harvesting ($n = 3$ in 1994; $n = 2$ in 1995; Table 1). Data classed by successional status were analyzed using general linear models (SAS, 1990). The least significant difference was used to compare the treatment means for early-, mid- and late-successional stands.

Pearson correlation analysis was used to test for correlations between microbial biomass concentrations (using µg active fungi, bacteria or both g^{-1} organic matter) and other forest floor variables, evaluated as significant at $P \leq 0.05$. Stepwise regression analysis was used to predict the variation in microbial biomass concentrations (µg microbial biomass g^{-1} organic matter), using successional status, soil moisture, forest floor mass, forest floor temperature, pH, NH_4^+ and NO_3^-, and total N and C (where applicable) as the independent variables. Significance was evaluated at $P \leq 0.05$. Nonlinear regression was used to fit a least squares polynomial (quadratic or cubic) curve to the data as a function of stand age. Variance components analysis was used to determine within stand, among stand and seasonal variance in microbial biomass.

Statistical analyses were performed using SAS (SAS, 1990) or JMP (SAS, 1995) statistical software.

3. Results

Stand and sampling period average amounts of active microbial biomass (fungi plus bacteria) ranged from 38 to 103 µg g^{-1} organic matter and 40 to 800 mg m^{-2} forest floor organic matter. Active bacterial biomass ranged among stands from 19 to 45 µg g^{-1} organic matter and 30 to 329 mg m^{-2} forest floor organic matter. Active fungal biomass ranged from 19 to 66 µg g^{-1} and 41 to 795 mg m^{-2} forest floor organic matter.

3.1. Trends in microbial biomass with successional status and stand age

Differences among successional groups in active microbial biomass (fungi plus bacteria) were variable in 1994. Active microbial biomass was significantly less in the early-successional stands compared to mid- and late-successional stands in June, but not in August and October (Fig. 1a–c). With the addition of three younger stands in 1995 (ages 3, 4 and 5), there was a consistent pattern of greater active microbial biomass

in early- and late-successional stands than in mid-successional stands (Fig. 1d–f). Fungi and bacteria varied independently: significant differences among successional groups were not necessarily common to bacteria and fungi (Fig. 1). We did not find any significant differences in the ratio of fungi to bacteria among successional groups.

When the data were graphed by stand age, the pattern of greater active biomass (fungi plus bacteria) in the youngest and oldest stands is again evident (Fig. 2). These visually apparent trends were supported by a significant fit ($P = 0.006$) for a quadratic polynomial ($R^2 = 0.42$; Fig. 2).

We calculated active microbial biomass (fungi plus bacteria) per unit area (g m^{-2}) to incorporate differences in forest floor organic matter among stands (Fig. 3). Active microbial biomass followed a similar pattern to that of forest floor mass (Fig. 3). The best curvilinear fit to forest floor organic matter as a function of stand age was a cubic polynomial ($P = 0.005$; $R^2 = 0.65$). A cubic polynomial was also significant for microbial biomass ($P \leq 0.000$) and explained similar variation ($R^2 = 0.72$), confirming that forest floor organic matter is an important factor controlling microbial biomass per unit area.

Seasonal trends in the amounts of active fungi and bacteria were not consistent between years. In 1994, active fungi were significantly more concentrated in October than in June or August (Fig. 1a–c). There were no significant differences in active fungi among sample dates in 1995. Active bacteria were not significantly different among sampling dates in 1994 (Fig. 1a–c). In 1995, active bacteria were significantly more concentrated in August than June (Fig. 1d and e). Variation in active fungi among sampling dates was greater than the variation among plots, as measured by variance components analysis. For active bacteria, variation among sampling dates was smaller than variation among plots.

3.2. Relationship between microbial biomass and environmental factors

Using regression analysis applied to samples from each stand pooled within year, we found that microbial biomass was not very responsive to any of the factors measured. Forest floor moisture content explained more of the variation in active fungal biomass (on a µg g^{-1} organic matter basis) than any other forest floor variable measured (temperature, pH, forest floor mass, NH_4^+, NO_3^-, total N, total C and C-to-N ratio) in both years. In 1994, moisture content, forest floor temperature and pH together explained only 23% of the variation in active fungal biomass ($P \leq 0.05$). Moisture was positively associated with active fungal biomass; temperature and pH were nega-
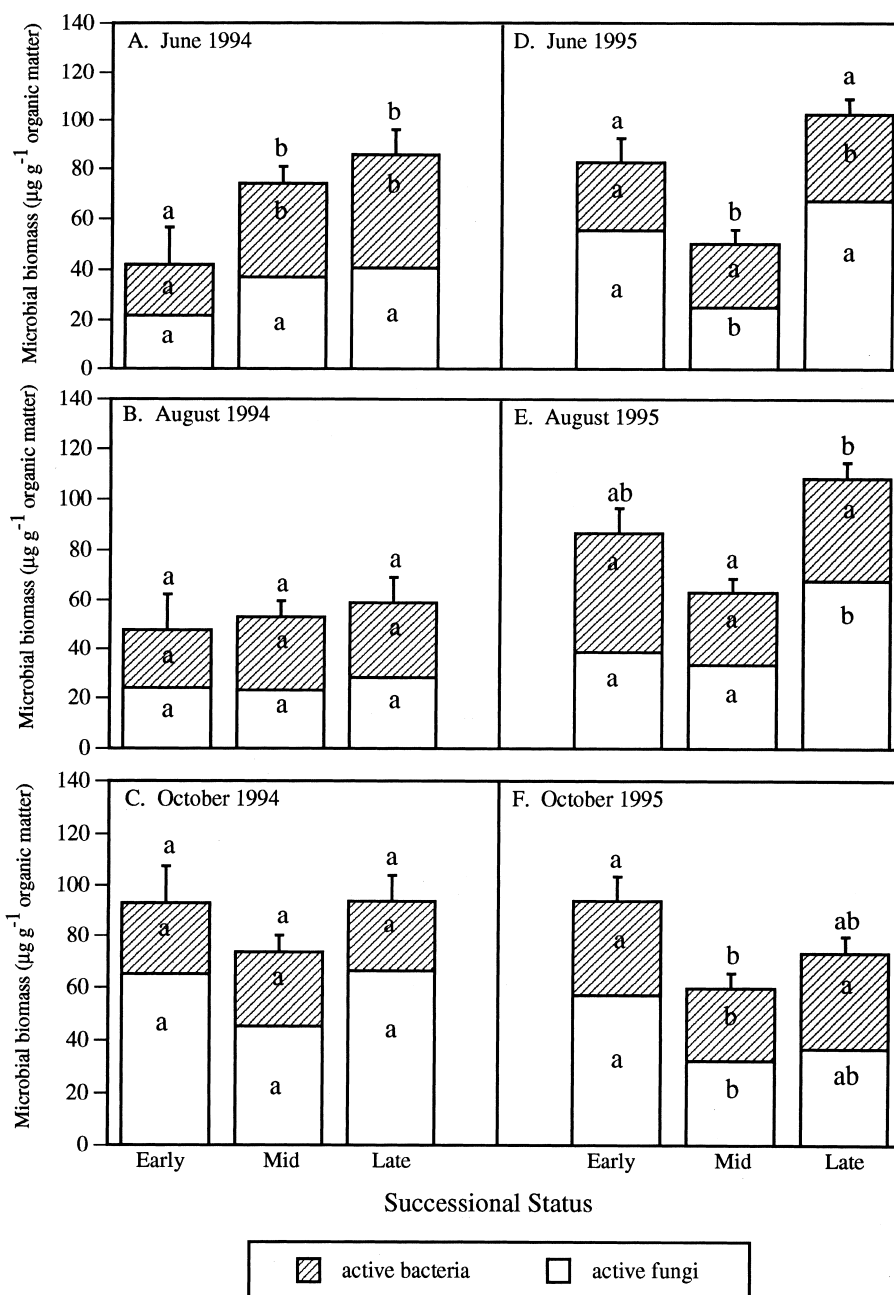
Fig. 1. Active fungal and bacterial biomass in the forest floors of northern hardwood stands by secondary successional status in June (A), August (B) and October, 1994 (C) and June (D), August (E) and October, 1995 (F). Standard errors are shown for fungi plus bacteria. Means with the same letter are not significantly different at $P \leq 0.05$.

tively associated with active fungi in 1994. In 1995, forest floor moisture content and successional status explained 27% of the variation in active fungi ($P \leq 0.05$). Less than 10% of the variation in active bacterial biomass was explained by the environmental variables we measured. Late-successional stands had significantly greater forest floor moisture content in both 1994 and 1995 than early- and mid-successional

stands. The significant effect of successional status in regression analysis corroborates these results.

Correlation analysis supported the results of the regression analyses. There was a consistent and positive correlation between forest floor moisture content and microbial biomass concentrations in 1994 and 1995, with R^2 ranging from 0.27 to 0.59 and $P \leq 0.05$. Forest floor mass was positively correlated with mi-
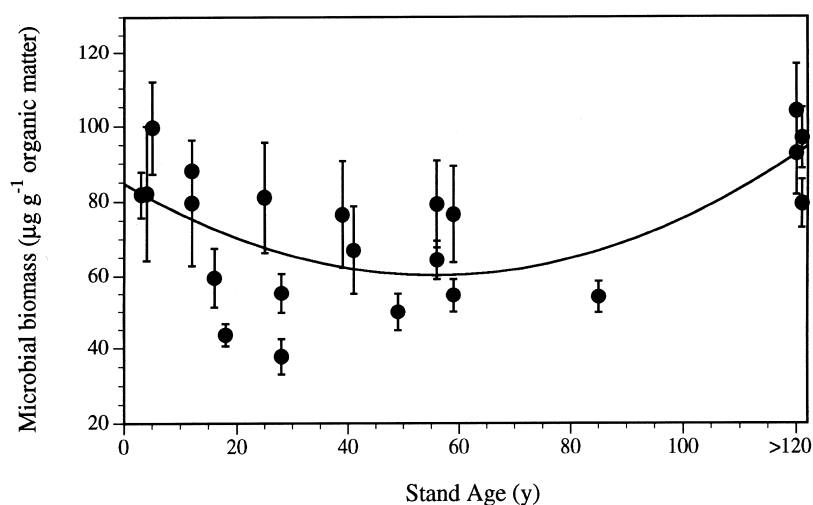
Fig. 2. Active microbial biomass (fungi plus bacteria) as a function of stand age in a northern hardwood successional sequence. Means and standard errors are based on three sampling periods in either 1994 or 1995.

crobial biomass, but this relationship was significant only for active fungi in 1994. There was a negative correlation between pH and active bacteria and between pH and active fungi plus active bacteria in 1995, with R^2 ranging from 0.23 to 0.29 and $P \leq 0.05$.

3.3. Forest floor N and C

In contrast to microbial biomass, NH_4^+ was greater in mid-successional stands than in early- or late-successional stands; the difference was significant in June and October of 1995. There was significantly more NH_4^+ in all stands in June than in August and October. Nitrate was detected in the youngest stand in the successional sequence, but was near zero in all other stands.

Forest floor total N was not significantly correlated with microbial concentrations in 1994 or 1995. Carbon-to-N ratios were highest in the youngest stands, declining to a low point in mid-succession, and rising in late succession (cubic polynomial, $P = 0.09$; $R^2 = 0.43$; Fig. 4).

4. Discussion

4.1. Comparison to other sites

The use of numerous methods for assessing microbial biomass in soil limits the comparison of studies. Even studies using the same methods may report results using different units. We compared the fungal and bacterial biomass measured in this study with measurements made using direct count methods in other forest and grassland ecosystems.

The range of active fungal and active bacterial biomass measured in this study was of the same order of magnitude as those measured in the organic horizons of clearcut and mature Scots pine stands in Sweden (Bååth, 1980; Lundgren, 1982). A 47-yr-old naturally regenerated Douglas fir stand on the Oregon Coast Range (Ingham and Thies, 1997) had very similar active bacterial biomass, but 100× higher active fungal biomass in the forest floor. A much lower microbial biomass in our study than in forest stands in the northwestern US was also borne out by comparison to sites with or without mycorrhizal mats in two additional stands in the Pacific Northwest (Ingham et al., 1991). Active fungal and bacterial biomass measured in mineral soils from riparian Douglas-fir, California black oak forests in Oregon (Griffiths et al., 1997) were very similar to that measured in our study even though microbial concentrations are generally much lower in mineral than in organic soil horizons. Fungal dominance of active microbial biomass in our northern hardwood stands was not nearly as pronounced as in the coniferous forests of the northwestern US (Ingham and Thies, 1997). High fungal biomass in northwestern forests may be attributed to the dominance by coniferous species, whose ectomycorrhizas tend to develop mycorrhizal mats, compared to the predominantly VA mycorrhizal northern hardwoods. As expected (see Zak et al., 1994), both fungal and bacterial biomass were much greater than in successional semiarid steppe communities and a nearby native plant community dominated by shortgrass prairie species (Klein et al., 1995).

4.2. Effects of forest succession on forest floor microbial biomass and N

In this study, active microbial biomass in young stands was quite similar to that in the oldest stands,
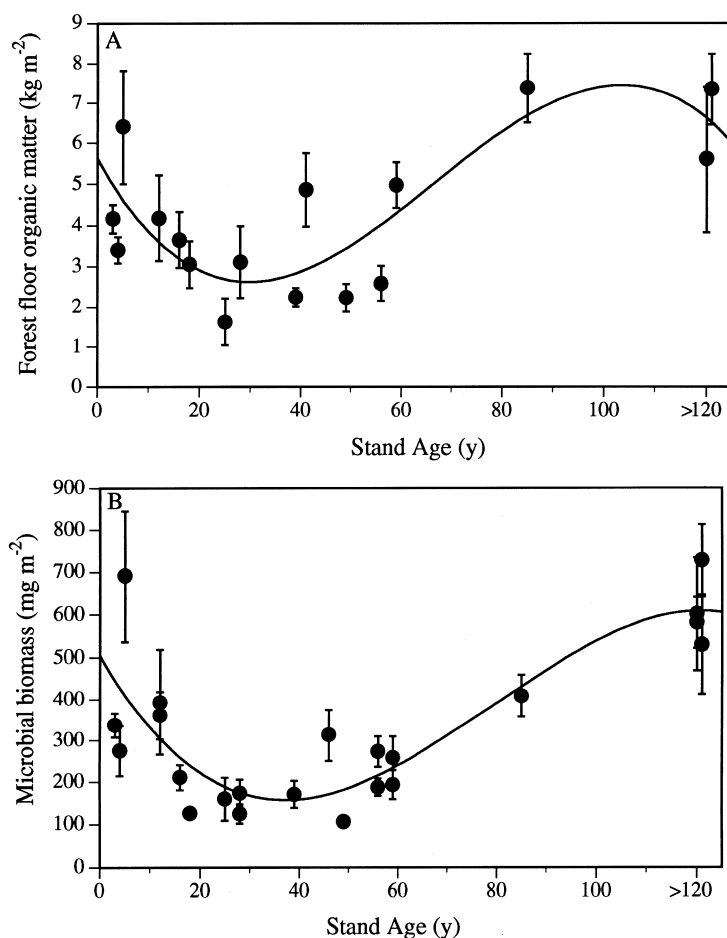
Fig. 3. Forest floor mass (A) and active microbial biomass ((B) fungi plus bacteria) as a function of stand age in a northern hardwood succes-
sional sequence. Mean forest floor mass and standard error for each stand are based on 5 transects per stand, sampled quantitatively at one time
during the study. Mean active microbial biomass and standard error are based on three sampling periods in either 1994 or 1995.

and higher than that in mid-successional stands
(Figs. 2 and 3). The similarity between young and old
stands suggests that the greatest changes in conditions
affecting microbial activity in the northern hardwood
forest occur in mid-succession. The short-term effects
of harvesting on microbial biomass documented by
Sundman et al. (1978), Bååth (1980), Lundgren (1982),
Hendrickson et al. (1985) and Ingham et al. (1993)
were not detected in our study. Transient effects of
harvesting on microbial biomass, if present, must have
disappeared within 3 y of harvesting, our earliest
measurement.

Microbial C content was higher in old-growth for-
ests compared to 3- and 10-yr-old forests planted fol-
lowing harvesting in British Columbia (Chang et al.,
1995). Soil moisture in the O$_e$ horizon was higher in
the old-growth forests than in the 3- and 10-yr-old
plantations (Chang et al., 1995). Our result is similar
to theirs in that our late successional stands had high
microbial biomass associated with high moisture con-
tent. Moisture content, coupled with organic fraction,
may help to explain high microbial biomass in late-

successional stands, but not differences between mid-
and early-successional stands, since differences in
moisture and organic fraction were variable among
sampling periods. Low forest floor organic fractions in
mid-successional stands may contribute to low moist-
ure content, both of which could contribute to the low
microbial biomass of the mid-successional stands.

Assessments of microbial biomass in relation to C
and N availability and aboveground net primary pro-
duction (ANPP) suggest that microbial biomass is
highly correlated with ANPP and C availability (Zak
et al., 1990, 1994). These studies were conducted in a
sequence of old fields in east-central Minnesota (Zak
et al., 1990), and with late-successional ecosystems
across a broad gradient of ANPP (Zak et al., 1994).
We did not find strong correlations between microbial
biomass and soil C, N, or C-to-N ratio. However, the
successional sequence in our study was complicated by
inputs of woody debris that are not present in old field
succession. In addition, the range of C content found
among our northern hardwood forest sites was much
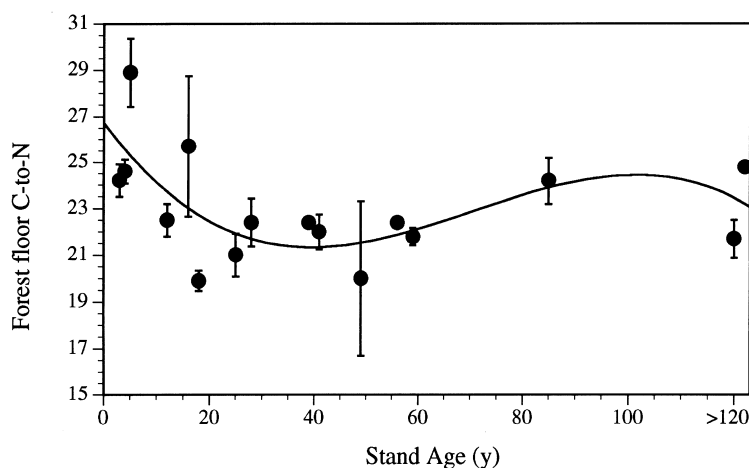smaller than that measured by Zak et al. (1990, 1994).

Fig. 4. Carbon-to-nitrogen ratio in the forest floor as a function of stand age in a northern hardwood successional sequence. Data are means and standard error of the June sampling period in either 1994 or 1995 for each stand.

An increase in the substrate available for decomposition, in the form of fine woody debris, and an increase in available nutrients following harvesting may contribute to high microbial biomass in early-successional stands. Entry et al. (1986) documented increased microbial biomass on harvested sites where logging residue remained, and attributed the increase to the large amount of organic matter available for decomposition. In our study, there was visibly more woody debris in the form of logging slash in the early-successional stands. In addition, higher concentrations of N and nonstructural carbohydrate in leaf litter of early-successional species in the northern hardwood forest (Hughes and Fahey, 1994) could contribute to greater microbial activity (Flanagan, 1986; Lekkerkerk et al., 1990) and potentially biomass.

Older stands may have higher nutrient availability than the early-successional stands because of reduced nutrient accumulation rates (Vitousek and Reiners, 1975), and this could contribute to high microbial biomass. Low amounts of microbial biomass in the mid-successional stands might therefore be attributed to greater competition for nutrients by rapidly growing vegetation. If this were the case, however, we would expect to see lower concentrations of NO_3^- and NH_4^+ in these stands. Instead, NH_4^+ in the forest floor was greatest in mid-successional stands. Logging slash may initially act as a sink for N, whereas once the C-to-N ratio of the wood has reached the stage where mineralization can occur, in mid-succession, woody debris becomes a source of N in the forest floor (Covington, 1981). High NH_4^+ concentrations in mid-succession might reflect a lower microbial immobilization capacity, if C, rather than N, is limiting microbial activity in these stands. A large pulse of dead pin cherry wood occurs at about 15 y after harvesting, coincident with increasing inputs of leaves with lower N concentration and higher structural carbohydrates than in

younger stands (Hughes and Fahey, 1994). Lower substrate quality could contribute to lower rates of decomposition and lower microbial biomass in mid-successional stands.

Higher soil concentrations of NO_3^- under the early-successional stands was due to higher concentrations in the youngest stand only. We did not find high microbial biomass in the youngest stand at times when NO_3^- was elevated. Higher nitrification in this stand could be a function of greater microbial turnover, rather than greater standing microbial biomass.

In conclusion, we found differences in microbial biomass at different stages of forest succession and identified forest floor moisture content as the environmental factor that most frequently explained variation in microbial biomass. However, soil moisture in combination with other measured variables explained only a small proportion of the variation and differed among successional groups in its importance. Our understanding of successional changes in microbial biomass in the northern hardwood forest might be improved by monitoring litterfall quantity and quality, including inputs of woody debris, which affect C and N dynamics and may in turn be important to microbial dynamics.

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