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Relationships between soil microbial properties and aboveground stand characteristics of conifer forests in Oregon

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Abstract. Eight forest sites representing a large range of climate, vegetation, and productivity were sampled in a transect across Oregon to study the relationships between aboveground stand characteristics and soil microbial properties. These sites had a range in leaf area index of 0.6 to $16\,m^2\,m^{-2}$ and net primary productivity of 0.3 to $14\,Mg\,ha^{-1}\,yr^{-1}$.

Measurements of soil and forest floor inorganic N concentrations and in situ net N mineralization, nitrification, denitrification, and soil respiration were made monthly for one year. Microbial biomass C and anaerobic N mineralization, an index of N availability, were also measured. Annual mean concentrations of NH_4^+ ranged from 37 to $96\,mg\,N\,kg^{-1}$ in the forest floor and from 1.7 to $10.7\,mg\,N\,kg^{-1}$ in the mineral soil. Concentrations of NO_3^- were low ($< 1\,mg\,N\,kg^{-1}$) at all sites. Net N mineralization and nitrification, as measured by the buried bag technique, were low on most sites and denitrification was not detected at any site. Available N varied from 17 to $101\,mg\,N\,kg^{-1}$, microbial biomass C ranged from 190 to $1230\,mg\,C\,kg^{-1}$, and soil respiration rates varied from 1.3 to $49\,mg\,C\,kg^{-1}\,day^{-1}$ across these sites. Seasonal peaks in NH_4^+ concentrations and soil respiration rates were usually observed in the spring and fall.

The soils data were positively correlated with several aboveground variables, including leaf area index and net primary productivity, and the near infrared-to-red reflectance ratio obtained from the airborne simulator of the Thematic Mapper satellite. The data suggest that close relationships between aboveground productivity and soil microbial processes exist in forests approaching semi-equilibrium conditions.

Abbreviations: IR – infrared; LAI – leaf area index; k_C – proportion of microbial biomass C mineralized to CO_2; NPP – net primary productivity; TM – Thematic Mapper

Introduction

Ecologists have become increasingly interested in nutrient cycling processes at the landscape and global scale. To interpret processes operating at such large scales, it is necessary to establish linkages between vegetation and soil components and fluxes of gases to the atmosphere.

Linkages between vegetation and soil include plant nutrient uptake and the return of senescent plant parts to the soil. In coniferous forest ecosystems, this cycling of nutrients between plants and soil is often tightly regulated, particularly for N (Vitousek 1982; Vitousek et al. 1988). Because growth of temperate forests is normally limited by N, aboveground biomass and productivity are often highly correlated with N availability (Shumway & Atkinson 1978; Ågren 1983; Pastor et al. 1984; Birk & Vitousek 1986). Similarly, the heterotrophic biomass of the forest floor and mineral soil is likely to be tightly coupled to primary productivity, which dictates the amount and quality of detritus returned to the soil. Despite the significant amount of data collected on the production of aboveground and belowground detritus in forest ecosystems (e.g., Vogt et al. 1986), little is known about the relationship between these inputs and the size or activity of the soil microbial biomass.

Carbon and N are lost from terrestrial ecosystems to the atmosphere by soil and plant respiration (CO_2 evolution) and denitrification. Although CO_2 fluxes have been studied extensively for many years (e.g., Reiners 1968; Schlesinger 1977; Schlentner & Van Cleve 1985) and more data is accumulating for denitrification (e.g., Robertson & Tiedje 1984; Davidson et al. 1989), it is difficult to generalize these processes to a large scale. The need to extrapolate these measurements is important for understanding the global impact of N and C cycle processes (Mooney et al. 1987).

To extrapolate discrete measurements of nutrient fluxes from a single location to a larger area requires well defined and consistent relationships between factors that control nutrient fluxes over different spatial scales. For example, some success in predicting CO_2 evolution at particular sites has been obtained using empirical models with temperature and moisture as driving variables (Reiners 1968; Schlentner & Van Cleve 1985), however, the applicability of such models for large areas has not been tested.

Recently Groffman and Tiedje (1989) demonstrated that annual N flux via denitrification was highly correlated to more stable features of the ecosystem, such as soil textural and drainage classes, but their approach needs wider testing if estimates of denitrification and related processes are to be made more general. Wissmar et al. (1982) show a high correlation between gross ecosystem productivity and ecosystem respiration in an analysis of vastly different aquatic and terrestrial ecosystems. In principle, this approach might be extended to other N and C cycle processes.

One of the more promising approaches for estimating nutrient cycling at large scales is through the use of remote sensing (e.g., Running et al. 1986;

Tucker et al. 1986; Peterson et al. 1987; Matson & Harris 1988). For example, Peterson et al. (1987) found that the near IR/red reflectance ratio of vegetation was highly correlated to the LAI of mature conifer forest stands, which in turn was correlated to potential photosynthesis and NPP (Waring 1983). It is possible that such remote sensing data may also be correlated with soil processes that are closely linked to aboveground processes.

There were two main objectives of this study. The first was to study the relationships between microbial biomass, soil respiration, various N transformations, and aboveground indicators of forest biomass and productivity. Secondly, we examined the possibility of using a remotely sensed variable (the ratio of near IR to red reflected spectral wavelength intensities) as an indirect indicator of soil microbial biomass and microbial activity.

Study sites

Eight mature coniferous forest sites, located on an east-west transect from the Pacific Ocean to central Oregon (Fig. 1), were used for this study. These sites were selected because they represented a wide range in vegetation, soil, climate, and topographic conditions, (Table 1) and have been extensively

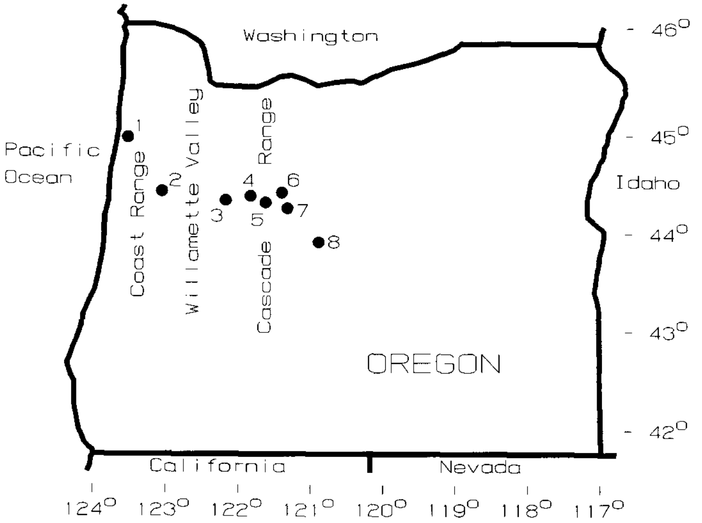

Fig. 1. Geographic location of the eight study locations (1–8) arranged along an east-west transect in Oregon.

Table 1. Site and soil characteristics of study areas along an east-west transect in Oregon.

Site	Dominant tree species	Basal area ($m^2 ha^{-1}$)	Soil greatgroup	Elevation (m)	Mean annual precipitation (cm)	Mean annual temperature (C)
1	*Tsuga heterophylla*	112	Haplohumult	268	253	10.3
2	*Pseudotsuga menziesii*	43	Xerocrept	229	108	11.1
3	*Pseudotsuga menziesii*	59	Xerumbrept	488	158	10.3
4	*Tsuga heterophylla* *Pseudotsuga menziesii* *Abies amabilis*	94	Haplohumult	1219	185	7.5
5	*Tsuga mertensiana*	63	Cryandept	1463	212	4.6
6	*Pinus ponderosa*	43	Vitrandept	914	26	8.6
7	*Pseudotsuga menziesii* *Abies concolor*	59	Vitrandept	1244	40	7.3
8	*Juniperus occidentalis*	24	Torriorthent	1317	26	6.3

characterized. More detailed descriptions of these sites can be found in Gholz (1982), Running et al. (1986), and Peterson et al. (1987).

Methods

Sampling

Soil sampling was generally done within one 0.25-ha (50 m square) plot at each site, with the exception that circular plots with a 30-m radius (0.28 ha) were used at sites 5 and 8. The two Coast Range sites (sites 1 and 2) were sampled on a monthly basis, beginning in November 1984; deep snow and impassible roads prevented sampling at some sites (sites 4, 5, and 7) in the Cascade Range during portions of the winter months. At each sampling time, three randomly oriented 30-m transects were established within each plot. Each 30-m transect was subdivided into a 10-m segment, and one soil sampling point was randomly located on each segment (Vitousek & Matson 1985). This gave a total of nine soil samples per site.

Data for aboveground stand characteristics (LAI and NPP) and remote sensing information (near IR (760–900 nm) to red (630–690 nm) reflectance ratio) obtained with an airborne simulator of the TM satellite are derived from previously reported work (Peterson et al. 1987), which provides a detailed description of methods.

N mineralization and nitrification

A buried bag technique was used to measure in situ N mineralization and nitrification rates (Pastor et al. 1984). One 6.5-cm diameter by 20-cm long soil core was taken at each sampling point and transferred into a polyethylene bag, which was sealed and placed into the same soil core hole. Care was taken to keep the soil cores intact; litter and mineral soil layers were not separated, preserving the natural soil horizon boundaries. Samples for determination of initial inorganic N concentrations of the forest floor and mineral soil were collected separately from along the wall of the soil core hold. These initial samples were placed in pre-weighed containers containing 100 mL of 2 *M* KCl (Gosz & White 1986). The buried bag samples were incubated for about a month (except for those that over-wintered), exhumed, and brought back to the laboratory where they were separated into forest floor and mineral horizons. About 10 g from each horizon was extracted for inorganic N using 100 mL of 2 *M* KCl. The remaining material from each horizon was used to determine water content by oven drying at 105 C for 24 hr. All KCl extracts were thoroughly mixed and allowed to settle for one day. A subsample of the clarified supernatant was removed for NH_4^+ and NO_3^- analysis. NH_{4+} (salicylate/nitroprusside method) and NO_3^- (diazotization following Cd-reduction) were determined colorimetrically using standard autoanalyzer techniques.

Denitrification and soil respiration

An impact coring device that minimized soil compaction, similar to that described by Robertson & Tiedje (1984), was used to extract soil cores encased in 2.5-cm diameter by 20-cm long acrylic tubes. Two cores, containing forest floor and mineral soil, were taken at each soil sampling point. Tubes were capped with rubber septa. One tube was injected with approximately 10 mL of C_2H_2, to block denitrification and allow N_2O to accumulate (Yoshinari & Knowles 1976); the other received 10 mL of air to measure natural N_2O production. Initial gas concentrations were determined in samples collected in 3-mL evacuated vials. The tubes were then returned to their respective holes, and incubated in situ for 18 to 30 hr. After the incubation period, the tubes were collected, head space gases were mixed using a 50-mL syringe, and gas samples were collected in 3-mL evacuated vials. The tubes were returned to the laboratory, where head space volume, water content, and total soil dry weight were determined. Head space volume was determined using a pressure transducer (Parkin et al. 1984). A gas chromatograph with a ^{63}Ni electron capture detector was used to measure concentrations of N_2O and CO_2 in the gas samples stored in evacuated vials (Parkin 1985). Differences between final and initial CO_2 and N_2O concentrations were used to calculate soil respiration and denitrification or N_2O production rates, respectively.

Available N and microbial biomass

Bulk samples for available N and microbial biomass determinations were collected from the top 20 cm of mineral soil in November 1984. Available N was determined using a modification of the anaerobic N mineralization method (Keeney & Bremner 1966) described by Myrold (1987). Microbial biomass C was determined using the chloroform fumigation-incubation technique (Jenkinson & Powlson 1976). The amount of CO_2 that accumulated over a 10-day incubation was measured. A k_C of 0.41 (Anderson and Domsch, 1978) was used to calculate biomass C. No control value was subtracted.

Results and discussion

Inorganic N concentrations at all sites were dominated by NH_4^+; only in the mineral soil at site 8, the most eastern site, did NO_3^- make up > 1% of the total inorganic N (Table 2). Concentrations of NH_4^+ in the forest floor were generally more than 20-fold higher than those found in the mineral soil. Forest floor NH_4^+ concentrations were highest near the coast (site 1) and at the low elevation site in the western Cascades (site 3), intermediate at sites 4 and 7, and lowest at sites 2, 5, 6, and 8 (Table 2). Concentrations of forest floor NH_4^+ were not significantly correlated with any stand characteristics.

Mineral soil NH_4^+ concentrations generally followed the same pattern among sites as forest floor NH_4^+, except that the lowest concentration was found at site 3. Concentrations of NH_4^+ in mineral soils were, however, significantly correlated to LAI, with higher concentrations in stands with greater LAI (Table 3). Mineral soil NH_4^+ concentrations were also positively correlated to other soil variables, e.g., microbial biomass C and soil respiration rates (Table 3).

Seasonal patterns were apparent in forest floor and soil NH_4^+ concentrations (Figure 2). Highest concentrations were measured in the spring or early summer with secondary peaks occurring at some sites in autumn. The timing of the spring peaks shifted from April near the coast (site 1) and in the interior slopes of the Coast Range (site 2) to July for the sites in the Cascades. This shift tracks the seasonal differences in temperature and moisture observed from the coast eastward into central Oregon (Gholz 1982).

Concentrations of inorganic N in forest floor and mineral soil compare

Table 2. Annual mean concentrations of forest floor and mineral soil NH_4^+ and NO_3^-. Values are the mean ± standard deviation of monthly means (Fig. 2) in mg N kg^{-1}.

Site	Forest floor		Mineral soil	
	NH_4^+	NO_3^-	NH_4^+	NO_3^-
1	92 ± 13	0.22 ± 0.15	10.7 ± 2.0	0.09 ± 0.05
2	37 ± 10	0.19 ± 0.17	2.6 ± 0.5	0.02 ± 0.01
3	96 ± 27	0.59 ± 0.34	1.7 ± 0.3*	0.02 ± 0.01*
4	80 ± 19	0.06 ± 0.05	3.4 ± 0.6	0.00 ± 0.00
5	57 ± 15	0.04 ± 0.03	3.3 ± 0.8	0.03 ± 0.02
6	50 ± 18	0.07 ± 0.04	2.2 ± 0.4	0.00 ± 0.00
7	83 ± 26	0.36 ± 0.19	3.7 ± 1.2	0.03 ± 0.03
8	**	**	2.4 ± 0.4	0.70 ± 0.31

* Adjusted for 40% coarse fragment content.

**There was no forest floor at site 8.

Table 3. Correlation matrix of remotely sensed, physiographic, climatic, stand, and soil characteristics. Statistics based on n = 7 for available N, microbial biomass C, and mean annual forest floor NH_4^+ concentration; n = 8 for all other variables.

	Elevation	Temperature	Precipitation	Near IR/red ratio	LAI	NPP	Mineral soil NH_4^+	Forest floor NH_4^+	Available N	Microbial biomass C	Soil respiration
Elevation	–	−0.96***	−0.30	−0.31	−0.42	−0.68	−0.37	−0.03	−0.77*	−0.61	−0.58
Temperature		–	0.11	0.33	0.36	0.62	0.24	0.08	0.66	0.41	0.49
Precipitation			–	0.71*	0.83*	0.71*	0.59	0.39	0.41	0.65	0.79*
Near IR/red ratio				–	0.82*	0.76*	0.35	0.68	0.25	0.21	0.69
LAI					–	0.86**	0.78*	0.67	0.41	0.68	0.96***
NPP						–	0.68	0.26	0.84*	0.82*	0.89**
Mineral soil NH_4^+							–	0.41	0.41	0.85*	0.88**
Forest floor NH_4^+								–	−0.24	0.05	0.57
Available N									–	0.78*	0.55
Microbial biomass C										–	0.83*
Soil respiration											–

*, **, *** indicate significance at the 0.05, 0.01, and 0.001 probability levels, respectively.

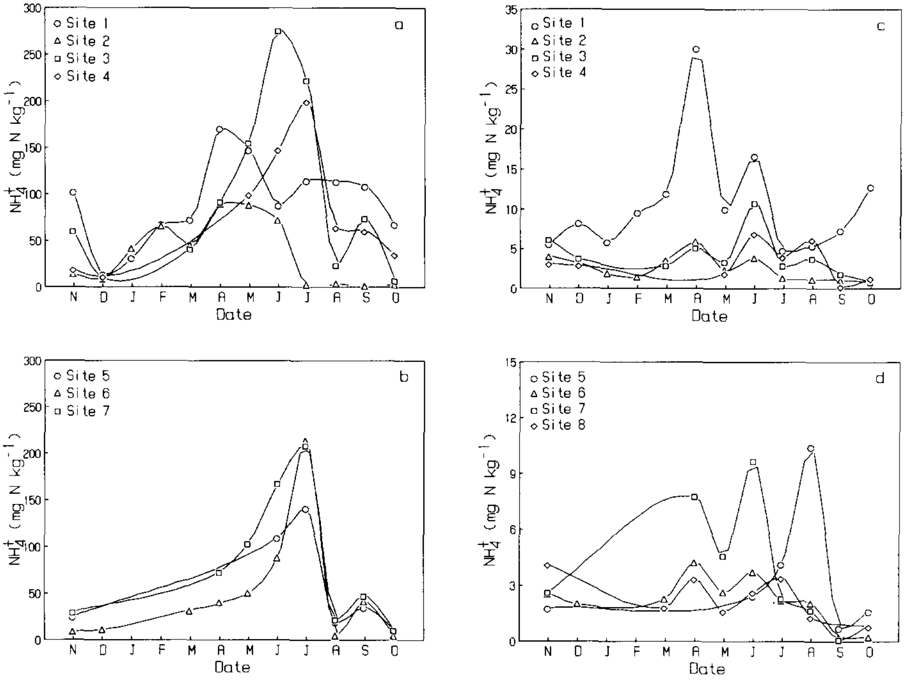

Fig. 2. Seasonal variations in mean forest floor (a and b) and mineral soil (c and d) NH_4^+ concentrations. Sample variability varied between < 10 to > 100% CV on a given date at a given site, but CV's were generally about 30% for forest floor and 20% for mineral soil NH_4^+ concentrations.

favorably with the data of Vitousek et al. (1982) for untrenched plots in western hemlock, Douglas-fir, and Pacific silver fir forest stands in Washington and Oregon. Vogt and Edmonds (1982) found similar concentrations of NH_4^+ in litter from low and high productivity stands of Douglas-fir in Washington. They observed higher concentrations of inorganic N in mineral soil (0–5 cm) than in the stands studied along the Oregon transect, but this is probably because we sampled to a 20-cm depth.

Net N mineralization and nitrification rates were inadequately quantified by the in situ buried bag technique. For many monthly periods, net N immobilization occurred in all sites (data not shown). This was most pronounced during the dry summer months. As a consequence, most sites showed annual net N immobilization, except for the forest floor at site 1 and mineral soil at sites 2 and 3, which had annual net N mineralization of $< 6\,\mathrm{kg\,N\,ha^{-1}}$. As indicated by the low NO_3^- concentrations (Table 2), nitrification rates were undetectable.

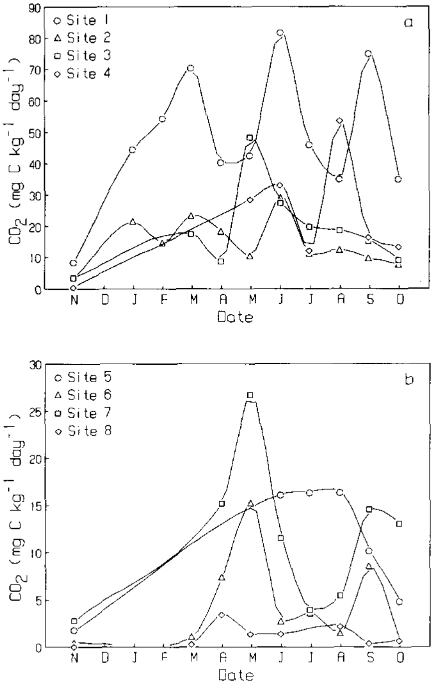

Fig. 3. Seasonal variations in mean daily soil respiration rates (a and b). Sample variability varied between < 10 to about 50% CV, but CV's were generally about 10%.

Soil respiration rates followed seasonal trends similar to those found with soil inorganic N concentrations. Highest rates were often measured in spring, with secondary peaks sometimes occurring in autumn (Fig. 3).

Mean daily soil respiration rates varied by a factor of almost 40, with the lowest rate at site 8, the most arid site, and the highest rate at site 1 near the coast (Table 4). This range in rates of CO_2 evolution brackets the rates measured by Vogt et al. (1980) for western hemlock, Douglas-fir, and Pacific silver fir sites in Washington, and is similar to soil respiration rates measured in other North American conifer forests (Ewel et al. 1987; Gordon et al. 1987; Schlentner & Van Cleve 1985; Weber 1985).

The relationships between CO_2 evolution, which includes microbial metabolism and some respiration from severed roots, and stand characteristics were striking (Fig. 4). Both LAI and NPP were highly correlated with soil respiration rates. This suggests a fairly strong linkage of autotrophic C cycling processes and belowground C metabolism. A similar relationship between gross primary production and ecosystem respiration was shown by Wissmar et al. (1982) for a range of aquatic and terrestrial ecosystems. Soil

Table 4. Remote sensing, stand characteristics, and soil properties used in correlation analysis.

Site	Near IR/red ratio	Leaf area index ($\mathrm{m^2\,m^{-2}}$)	Net primary production* ($\mathrm{Mg\,ha^{-1}\,yr^{-1}}$)	Soil respiration rate** ($\mathrm{mg\,C\,kg^{-1}\,day^{-1}}$)	Available soil N ($\mathrm{mg\,N\,kg^{-1}}$)	Soil microbial biomass ($\mathrm{mg\,C\,kg^{-1}}$)
1	7.46	15.5	14	48.8 ± 1.7	82.6 ± 8.8	1230 ± 40
2	5.77	4.70	10.5	15.0 ± 0.9	101 ± 2	704 ± 50
3	7.46	7.56	6.2	19.0 ± 1.2	40.0 ± 1.7***	296 ± 11***
4	8.88	11.2	9.5	22.8 ± 2.4	51.6 ± 2.1	390 ± 11
5	5.55	5.45	4.2	11.0 ± 1.2	33.4 ± 1.4	488 ± 33
6	2.97	2.78	2.2	4.63 ± 0.91	29.0 ± 3.3	316 ± 35
7	6.27	5.34	4.9	11.7 ± 1.4	16.8 ± 1.0	187 ± 8
8	0.908	0.634	0.3	1.32 ± 0.25	–****	–****

* Based on Gholz (1982)

** Mean ± standard deviation of mean monthly rates (Fig. 3)

*** Adjusted for 40% coarse fragment content

**** Not determined

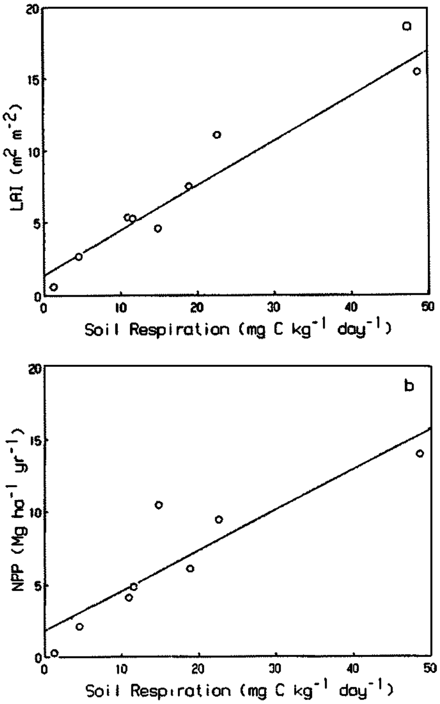

Fig. 4. Correlations between mean daily soil respiration rates and leaf area index (a) and net primary productivity (b).

respiration activity also was positively correlated with soil microbial biomass, the primary agent of C metabolism in soil, and precipitation, an important environmental factor influencing the activity of soil microorganisms.

Denitrification or N_2O production were not detected at any site on any sampling date. Since our detection level ($< 0.1\,g\,N\,ha^{-1}\,day^{-1}$) was quite sensitive, we believe that very little N is lost from these mature coniferous forests through biological N gas production. This is consistent with most of the data collected on these processes in coniferous forests (Davidson et al. 1989). For the higher or drier sites, this appears to be caused by the lack of a significant biomass of denitrifying bacteria; the wetter, more moderate sites in the Coast Range and west side of the Cascades seem to be limited by NO_3^- availability (Vermes & Myrold unpublished data).

Available soil N ranged from $17\,mg\,N\,kg^{-1}$ at site 7 to $101\,mg\,N\,kg^{-1}$ at site 2 (Table 4). According to Shumway & Atkinson (1978), Douglas-fir at site 7 would likely respond to N fertilization, whereas ponderosa pine (Powers 1980) is on the borderline of N deficiency. Sites 1 and 2 in the Coast

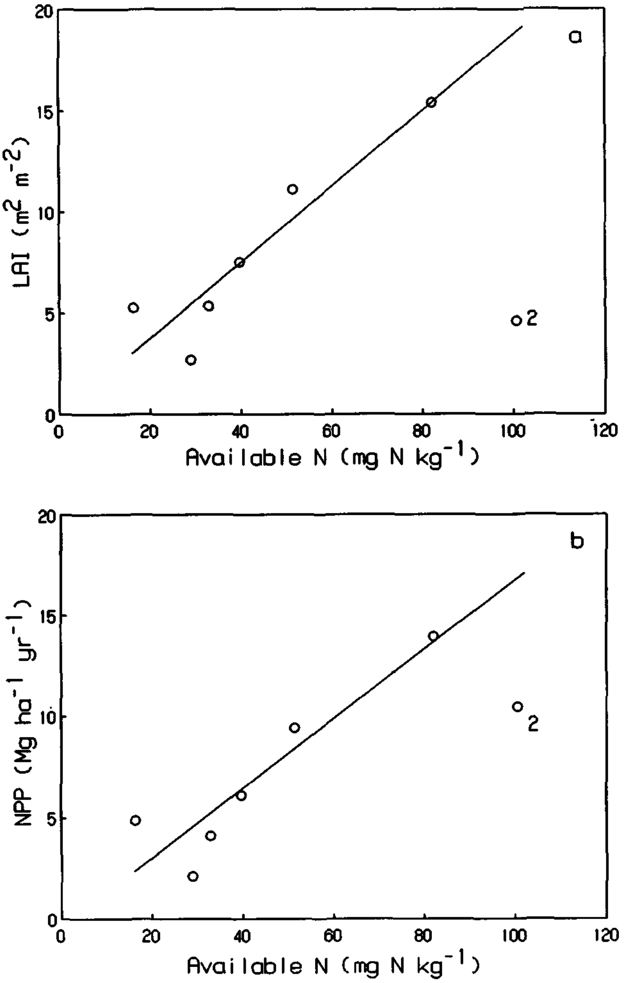

Fig. 5. Relationships between available soil N and leaf area index (a) and net primary productivity (b). Regression lines exclude the datum for site 2.

Range are probably not N deficient; all other sites would be intermediate. These trends in available N generally coincide with mean soil NH_4^+ concentrations (Table 2), although the best correlation among the soil variables was with microbial biomass C (Table 3). A high correlation between the anaerobic N mineralization assay and microbial biomass as measured by the chloroform fumigation-incubation method probably results because both methods measure the mineralization of recently killed microbial biomass (Myrold 1987).

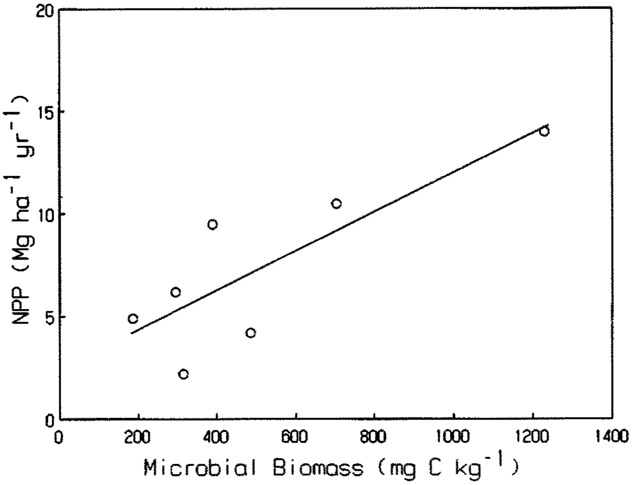

Fig. 6. Correlation between soil microbial biomass and net primary productivity.

Available soil N was positively correlated with aboveground stand characteristics (Table 3), especially NPP (Figure 5). The relationship between available soil N and LAI and NPP is better when the data from site 2 are excluded from the analysis ($r = 0.94$ and $r = 0.93$, respectively). Two reasons why site 2 does not follow the trend between available N and aboveground characteristics, which is displayed by the other sites along the transect, may be that tree growth is not N limited at this site and that site

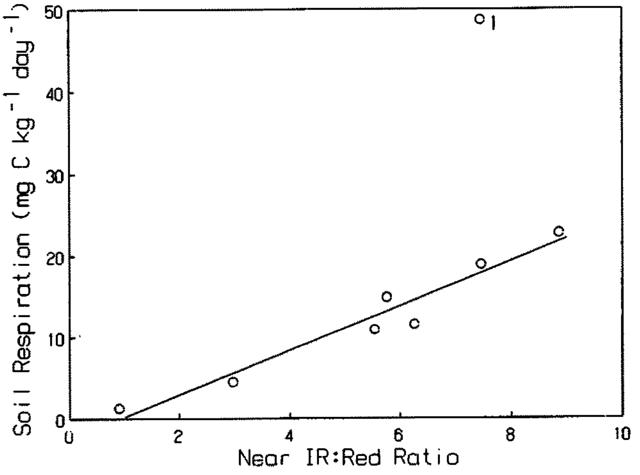

Fig. 7. Relationship between near IR/red ratio and mean daily soil respiration rate. Regression line excludes the datum for site 1.

2 has a much lower tree density (Peterson et al. 1987). The open nature of the stand at site 2 (e.g., 230 stems ha^{-1} vs. 2010 and 500 stems ha^{-1} at sites 1 and 3, respectively) results in a relatively low LAI - even under good conditions a tree can carry only so many leaves. The aboveground NPP of site 2 is relatively high in comparison to its LAI, perhaps because of a greater proportion of C allocated aboveground on fertile sites (Vogt et al. 1987) and enhanced photosynthesis due to 20% higher foliar N concentrations than in other sites along the transect (Peterson, unpublished data; Brix 1971). Higher foliage N concentrations at site 2, and consequently lower C:N and lignin:N ratios in the foliage, probably are partly responsible for the large amounts of available N at this site (Gosz 1981).

Microbial biomass C followed similar trends among sites to those exhibited by soil respiration and available soil N (Table 4). The highest level of microbial biomass was found at site 1 on the coast with microbial biomass generally decreasing eastward along the transect to the lowest level at site 7. Microbial biomass was significantly correlated with NPP but not with LAI (Fig. 6).

The correlations between the near IR/red reflectance ratio and the soil biological variables measured were not as strong as those found for aboveground vegetation measurements (Table 3), however the relationship with soil respiration was quite good (Fig. 7). The correlation of soil respiration rates with the near IR/red reflectance ratio becomes highly significant when the datum for site 1, the highly productive coastal site, is excluded ($r = 0.97$). The fact that the near IR/red reflectance ratio asymptotically reaches an upper limit at high LAI's may be partly responsible for the apparently anomalous datum for site 1 (Peterson et al. 1987).

Results of Running et al. (1986) suggested that remotely sensed data, particularly the near IR/red reflectance ratio, were correlated with the regional scale variations in aboveground biomass variables such as LAI, and less so, foliar biomass. Gholz (1982) had previously shown that aboveground NPP was directly correlated with LAI at this scale. Peterson et al. (1987) later showed that both single reflectance bands and band ratios of near IR to red reflectance were asymptotically related to LAI but not tree density. A close relationship between aboveground volume, basal area, and LAI led to a somewhat weaker relation between the spectral data and volume for the sites studied. A.H. Strahler (personal communication) has recently shown that the local variance in TM bands could be related to the local variation in tree density, crown size, and height using a geometric optics radiation transport model (Li & Strahler 1985). When these findings are coupled with the good relationships between soil parameters and aboveground vegetation indices illustrated in this paper, it seems likely that soil parameters might also be estimated empirically from remotely sensed data.

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