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Limitations to carbon mineralization in litter and mineral soil of young and old ponderosa pine forests

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Abstract

Summer drought is a feature of the semi-arid region of central Oregon, USA, where vegetation naturally develops into ponderosa pine (*Pinus ponderosa* var. Laws) forest. Forest management consists of clearcut harvest and natural regeneration. Soil microbial activity is interconnected with forest processes because substrate quality and availability can be important driving variables. Stand development influences the soil water regime, and water availability may also limit microbial activity. We determined factors limiting litter and mineral soil carbon (C) mineralisation rates in undisturbed old growth and regenerating (hereafter, young) ponderosa pine stands under a semi-arid climate. Mass of litter and dead fine roots did not differ significantly between the stands, but litter substrate quality was different. Young stand litter had significantly higher concentrations of total nitrogen (N), extractable organic N, extractable C, and microbial C and N than that from the old stand, probably because of litter fall from the broadleaved shrub understorey, including the N-fixing species *Purshia tridentata* (Pursch) DC, that comprised 40% of the young stand's leaf area. The old stand contained no understorey. For litter samples from the two stands, wetted to 60% of water-holding capacity (WHC), net mineral-N and CO_2–C mineralisation rates were similar despite the substrate quality differences. Mineral soil properties at 0–0.1 m depth were similar in the two stands, except for lower CO_2–C production in samples from the young stand; at 0.1–0.5 m depth, total C and N and microbial N concentrations were higher in the young stand. Net mineral-N production in field-moist soil, sampled during a typical summer drought and incubated at 25 °C for 56 days, was generally 3–6 mg kg^{-1} soil at both sites, but increased up to 29 mg kg^{-1} upon wetting to 60% of water-holding capacity. Over 56-day-long incubations, wetting also increased litter and soil microbial respiration rates by factors of about 500 and 3, respectively. The incubations yielded a proportionality between respiration rate and water content that was supported by in situ measurements of soil respiration in the young stand, before and after irrigation. A hypothetically wet year without soil water deficit caused a 2.5-fold increase in a modelled estimate of the young stand's annual soil respiration rate. Litter and soil C mineralisation rates in these ponderosa pine forests thus appeared to be limited much more by the availability of water than by a lack of available C or N substrates.

Keywords: Respiration; Drought; Pine forest; Litter; Nitrogen mineralisation

1. Introduction

Soil microbial activity is connected with plant processes, such as carbohydrate allocation to roots

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(Högberg et al., 2001), because substrate quality and availability can be important driving variables (Fitter et al., 1998; Craine et al., 1999; Vance and Chapin, 2001). Likewise, variable species composition and climate create spatial and temporal heterogeneity in substrate availability for microbial decomposition (Law et al., 2001a). In the semi-arid climate of central Oregon, USA, natural vegetation succession and recurrent fire eventually lead to open stands of ponderosa pine (*Pinus ponderosa* Var. Laws) with little understorey vegetation. These pines may be harvested by clear cutting and they are typically re-established by natural regeneration. The population and activity of soil microorganisms may thus be subject to a land-use change combining natural and anthropogenic processes. Here, we compare soil carbon (C) and nitrogen (N) pools and microbial activity in samples from an undisturbed, old-growth ponderosa pine forest and a nearby (young) stand that was harvested 22 years ago. Because of the semi-arid climate, we focus on the soil respiratory response to wetting following drought.

Soil water content is an abiotic variable that can greatly influence respiration rate, including that of roots and heterotrophic microorganisms in the rhizosphere (Burton et al., 1998; Kelliher et al., 1999; Irvine and Law, 2002). When soil is relatively dry, microbial activity increases strongly with water availability (Fang and Moncrieff, 2001; Howard and Howard, 1993). In forest litter, O'Connell (1990) found that microbial respiration rate was most responsive to water content from ca. 0.50 to 0.35 $m^3\ m^{-3}$. Reichstein et al. (2003) analyzed data from 17 forest and shrubland sites in North America and Europe and determined that relative soil water content, expressed as a fraction of field capacity, was a good predictor of water availability and, combined with temperature and leaf area index, it explained more than 60% of the daily variation in soil respiration across sites. However, the empirical model could not account for decomposition dynamics associated with site history and disturbance (e.g. clear-cutting). These independent studies suggest that further research is needed to determine the relative importance of water availability and disturbance on microbial activity.

In this paper, our goal was to determine factors limiting soil microbial activity in undisturbed old growth and regenerating ponderosa pine stands under the semi-arid climate of central Oregon. To examine substrate quantity and quality, we compared litter and mineral soil C and N pools and their properties. To quantify the effects of water availability, we measured C and N mineralisation rates of summer-dry samples and of the same samples re-wetted to 60% of water-holding capacity (WHC). In the regenerating stand, we also conducted a field watering experiment and used the model of Irvine and Law (2002) to compare soil respiration rates during a typically dry and hypothetically wet year.

2. Materials and methods

2.1. Description of sites

Samples of litter and mineral soil were collected in a young ponderosa pine forest and an old growth stand, 5 km away, in central Oregon, USA (44°26′N, 121°34′W, elevation 1188 m) during July 2000. The semi-arid climate is characterized by annual photosynthetically active irradiance of 2481 MJ m^{-2}, mean air temperature of 7.5 °C and precipitation of 552 mm (1999 data; Law et al., 2001b). The old stand is relatively undisturbed and very open (the one–sided leaf area per unit ground area, known as the leaf area index, was 2.1 in 2000), with sparse understorey vegetation (Law et al., 2001b). There were two size classes of trees that, respectively, averaged 50 and 250 years old, 555 and 72 stems ha^{-1}, 10 and 34 m tall, and 0.1 and 0.6 m diameter measured at a height of 1.3 m. The soil, originating from the Mount Mazama volcanic eruption of around 10,000 years ago, is classified as an Alfic Vitrixerand (Soil Survey Staff, 1998, http://www.ftw.nrcs.usda.gov/ssur_data.hmtl), and has a sandy loam texture that is consistent to 1.0 m depth (65% sand, 25% silt and 10% clay in the upper 0.2 m and 63% sand, 26% silt and 11% clay at 0.5–1.0 m depth).

The young stand was previously an old-growth forest, clearcut in 1978, and naturally regenerated. The average age of trees in 2000 was 15 ± 1 years and they were 4 m tall. There were two size classes based on stem diameter (> or <0.05 m) at a height of 1.3 m. The larger size class of 280 trees ha^{-1} had an average stem diameter of 0.1 m at a height of 1.3 m, while the others of density 975 ha^{-1} averaged 0.064 m at ground level. Broadleaved understorey shrubs averaged 1 m

tall. The evergreen manzanita (*Arctostaphylos patula* Greene) and deciduous bitterbrush (*Purshia tridentata* (Pursch) DC) accounted for about 10 and 30% of the total leaf area (1.0 when expressed as a one-sided leaf area index in July 2000; Law et al., 2001a), respectively, while the pine comprised 60%. The Alfic Vitrixerand soil was very similar to that in the old stand. However, silt and clay fractions increased with depth (69% sand, 26% silt, 5% clay in the upper 0.2 m, and 54% sand, 35% silt, 11% clay at 0.5–1.0 m depth). The soil is very permeable and porous, with a predominance of large pores emptying with relatively little suction, facilitating rapid drying by drainage and evaporation (Law et al., 2001a).

2.2. Soil sampling and analyses

Samples of litter and mineral soil were collected on 25 July 2000, the seventh day after rainfall during a typical summer drought that included only 6 mm fall for the previous 24 days. The litter was relatively undecomposed and consisted predominantly of needles and a few dicotyledonous leaves and small pieces of wood. It was collected by hand at 10 m intervals along each of three 50 m long, randomly located transects and pooled, with composite samples from each transect taken for analysis. To compare substrate availability in the two stands, litter mass per unit ground area was determined from 15 samples taken along similar transects in August 2001 (Sun et al., 2004). Mineral soil was sampled at the same locations with a 0.025 m diameter corer at depths of 0–0.1 m, 0.1–0.3 m and 0.3–0.5 m. The samples were transported to New Zealand at ambient temperature over 8 days and then placed at 4 °C. The litter was cut into 20–50 mm pieces and passed through a 5.6 mm sieve, and the mineral soil was passed through a 2 mm mesh. These field-moist samples were stored at 4 °C for up to 7 days before commencement of the biochemical measurements. Measurements were made in the young stand on 23 August 1999 and 23 July 2000 of temperature and bulk density at the three depths of mineral soil so that the laboratory-based respiration rates (see below) could be estimated on an area basis under field conditions.

Methods for the determination of pH, WHC, total C and N, extractable C, microbial C and N, and mineral-N (min-N=NH_4^+–N+NO_3^--N) concentrations are described by Ross et al. (1999a), and extractable organic N by Ross et al. (1999b). To calculate microbial C from the extractable-C flush value in the fumigation-extraction method, a k_{EC}-factor of 0.41 was applied, based on the value in Sparling et al. (1990) and adjusted for the determination of extracted C by a Shimadzu TOC-5000 total C analyser rather than by dichromate oxidation.

We determined carbon dioxide (CO_2–C) and net min-N production with both field-moist samples and samples wetted to 60% of water-holding capacity (WHC), using 5.0 g litter and 15.0 g mineral soil contained in 125 ml polypropylene containers incubated for 56 day at 25 °C. Incubations for CO_2–C production were in 1 l sealed glass jars fitted with a septum. The jars contained 10 ml water, except for those with field-moist litter, to maintain humidity and thus minimise evaporation from the sample. The jars were vented after each CO_2 measurement made with a Carle 8700 gas chromatograph. The jars with field-moist litter did not contain water because initial experiments showed that CO_2–C production increased appreciably with time, probably because of water absorption from the jar's humid air. This did not happen with the mineral soil samples. During the incubations, no adjustments were made for evaporation from the samples. However, a previous study with mineral soil from a New Zealand pine forest showed that water content decreased by only 2–3% of WHC when the samples were wetted to 60% of WHC and incubated similarly for 42 days at 25 °C (D.J. Ross, N.J. Rodda, J.A. Townsend, unpublished data). Incubations for net min-N production were done according to Scott et al. (1998).

2.3. Field watering experiment

The response of soil respiration rate to water amendment was determined in situ in the young stand. Measurements were made with an infrared gas analyzer (model LI6400, LICOR, Lincoln, NE, USA) connected to a chamber of sampling area 0.007 m^2, sealed onto a collar inserted in the soil. On 5 July 2000, we also installed five pairs of 0.19 m diameter, plastic collars in the soil to a depth of 0.03 m approximately 1 m from tree stems (the average tree crown radius was 1.2 m). One collar served as a control, and the other collar was watered twice. The sparse litter

present in some of the collars was carefully removed to focus on respiration response in the mineral soil. Inside each collar, we then inserted a 0.1 m diameter plastic collar, also to a depth of 0.03 m. On 7 July, we very slowly irrigated one of the paired collars with an equivalent of 27 mm rainfall and then measured soil respiration rate. About 1 h afterwards, there was 1.8 mm rain and we conducted a second set of respiration measurements. Further measurements were made on 8 and 10 July. A second irrigation of 34 mm was done after the 10 July measurements. Respiration measurements were made following that irrigation, and 2 days later.

2.4. Statistical analyses

Laboratory data are presented as means and standard deviations of the three samples and expressed on an oven-dry (105 °C) basis, unless otherwise stated. In statistical comparisons, the weakly significant value of $P < 0.10$ is included because of the small number of replicates and anticipated high spatial variability of soil properties that can occur in pine forests (Ruark and Zarnoch, 1992).

In the mineral soil, the significance of differences in soil properties with depth was assessed separately for each stand by a one-way analysis of variance (SYSTAT, 1996). The significance of site differences in litter and mineral soil properties at each sampling depth, and of differences in microbial respiration and net N-mineralization rates following wetting, was assessed by *t*-tests (SYSTAT, 1996). For the percentage of min-N present as NO_3^-–N, an arcsine square-root transformation was done. Linear regression was used to determine the significance of relationships between CO_2–C production and net min-N production.

3. Results

3.1. Litter and mineral soil properties

Litter quantity was not significantly different between the two stands even though the young stand was considered to be aggrading (Sun et al., 2004). Fine litter mass averaged 908 ± 161 g C m^{-2} in the young stand, and 860 ± 134 g m^{-2} in the old stand. Dead fine root mass in the top 1 m of mineral soil was not significantly different in the two stands (137 ± 69 g C m^{-2} in the young stand, versus 166 ± 55 g C m^{-2} in the old stand).

On 25 July, the litter in both stands was very dry and acidic. The field-moist litter water contents were equivalent to only 4% of WHC. The total C concentration of the litter was similar in the two stands

Table 1
Properties of litter and mineral soil sampled on 25 July 2000 beneath two stands of *Pinus ponderosa*, Metolius, Oregon, USA

Sample	pH	Water content		Total C (g kg^{-1})	Extractable C (mg kg^{-1})	Microbial C (mg kg^{-1})	Total N (g kg^{-1})	Mineral N (mg kg^{-1})	Extractable organic N (mg kg^{-1})	Microbial N (mg kg^{-1})
		(Field-moist) (g kg^{-1})	(60% of WHC) (g kg^{-1})							
Young stand										
Litter	4.5 (0.3)	71 (5)	1200	481 (11)	3280 (830)	12770 (2390)	8.5 (0.6)	6.4 (1.8)	104 (21)	674 (92)
Mineral soil										
0–0.1 m	6.5 (0)	40 (2)	237	23 (1)	82 (3)	251 (31)	0.89 (0.01)	2.3 (0.1)	9.6 (1.1)	22 (1)
0.1–0.3 m	6.8 (0)	66 (1)	213	9.9 (0.3)	38 (1)	159 (13)	0.47 (0.01)	1.3 (0.2)	5.8 (0.5)	13 (1)
0.3–0.5 m	6.9 (0.1)	86 (2)	199	8.0 (0.3)	32 (3)	111 (1)	0.42 (0.01)	0.9 (0.4)	4.6 (0.9)	11 (4)
Old stand										
Litter	4.3 (0.2)	67 (7)	1130	474 (71)	1780 (430)	7830 (2010)	7.2 (0.6)	4.3 (1.0)	71 (12)	404 (65)
Mineral soil										
0–0.1 m	6.8 (0.1)	40 (1)	247	23 (4)	83 (1)	291 (5)	0.89 (0.3)	2.1 (0.6)	9.9 (1.1)	26 (5)
0.1–0.3 m	7.0 (0)	83 (1)	218	8.0 (0.3)	44 (3)	119 (12)	0.43 (0.02)	1.1 (0.3)	7.5 (1.2)	11 (2)
0.3–0.5 m	7.1 (0)	100 (1)	214	6.4 (0.4)	35 (4)	85 (11)	0.36 (0.01)	0.6 (0.1)	7.9 (1.5)	10 (4)

Values are means with standard deviations in parentheses.

(Table 1). However, the young stand's litter tended to have higher concentrations of extractable and microbial C and total, extractable organic and microbial N ($P < 0.10$). There was also significantly more ($P < 0.05$) microbial C as a percentage of total C (2.7 versus 1.7%) and microbial N as a percentage of total N (7.9 versus 5.6%) in litter from the young than from the old stand.

In the mineral soil, property values were predictably highest at the 0–0.1 m depth, except for water content and pH (Table 1). For the 0–0.1 m depth soil, water content was equal in the two stands, and equivalent to only 10 % of WHC (0.05 $m^3\ m^{-3}$; computed using the measured bulk density of 1180 kg m^{-3}), and thus minimal. According to a water release curve expressed as ψ (MPa) $= -0.005\ (\theta/0.3)^{-5.4}$ (Law, unpublished data), the soil can hold around $\theta = 0.3\ m^3\ m^{-3}$ of water against gravity, but the matric potential ψ at sampling was −79 MPa. At 60% of WHC (0.29 $m^3\ m^{-3}$), the matric potential was −6 kPa or close to the −5 kPa value suggested earlier for sandy soils (Ross, 1989).

Soil total C and N concentrations were similar in both stands at 0–0.1 m depth, but over 0.1–0.5 m depth were higher ($P < 0.05$) in the young stand. The percentages of microbial C in total C (1.1–1.6%) and of microbial N in total N (2.5–2.9%) did not, however, differ significantly in the two stands, and were generally similar to those found in other sandy soils (Ross et al., 1999a,b). Microbial-C-to microbial N ratios ranged from 8.5 to 12.2 and were mainly higher than those found elsewhere by Ross et al. (1999a,b), suggesting that the microbial populations may have been enriched in fungi (Anderson and Domsch, 1980).

3.2. Nitrogen mineralization

In field-moist litter, net min-N production over 56 days at 25 °C was about two-fold greater ($P < 0.05$) in the young-stand than the old-stand samples (Table 2). Net NO_3^-–N production was low but, as a percentage of min-N at 56 days, was also greater ($P < 0.01$) in the young stand. Net min-N production of the litter increased appreciably after wetting to 60% of WHC and was then similar in the two stands; NO_3^--N was not detected.

Net min-N production in field-moist mineral soil did not generally vary significantly in the two stands, except at 0.1–0.3 m depth where production at 60% of WHC was greater ($P < 0.01$) in samples from the young stand (Table 2). Up to half of the min-N was oxidised to NO_3^-–N in the 0–0.1 m depth sample, but the percentage oxidation was minimal over 0.1–0.5 m depth. Min-N production rate increased four- to

Table 2
Net mineral N production on a dry weight basis, and production rate on a total N basis, during 56-day-long incubations at 25 °C of field-moist samples and samples wetted to 60% of water-holding capacity (WHC); also shown are percentages of min-N present as NO_3^--N at 56 days

Sample	Net min-N production (mg kg^{-1} sample)		Net min-N production rate (mg kg^{-1} total N h^{-1})		NO_3^-–N (% of min-N)	
	Field-moist	60% of WHC	Field-moist	60% of WHC	Field-moist	60% of WHC
Young stand						
Litter	12.0 (1.0)	27.0 (8.0)	1.1 (0.2)	2.4 (0.8)	10 (2)	0 (0)
Mineral soil						
0–0.1 m	3.9 (1.7)	21.0 (2.0)	3.3 (1.4)	17.5 (1.4)	47 (10)	87 (1)
0.1–0.3 m	6.3 (3.3)	5.7 (0.2)	9.9 (5.0)	9.0 (0.1)	7 (6)	34 (12)
0.3–0.5 m	0.7 (2.4)	4.1 (1.4)	1.2 (4.4)	7.4 (2.7)	3 (5)	37 (28)
Old stand						
Litter	5.8 (2.5)	29.0 (2.0)	0.6 (0.2)	3.0 (0.3)	3 (1)	0 (0)
Mineral soil						
0–0.1 m	5.5 (1.0)	21.0 (2.0)	4.7 (1.0)	17.8 (2.2)	41 (6)	93 (10)
0.1–0.3 m	2.6 (0.1)	3.4 (0.4)	4.5 (0.4)	6.0 (0.7)	3 (1)	11 (5)
0.3–0.5 m	3.1 (0.4)	3.3 (0.4)	6.1 (1.0)	6.9 (1.0)	2 (2)	3 (2)

Values are means with standard deviations in parentheses. Litter and soil were sampled on 25 July 2000 beneath two stands of *P. ponderosa*, Metolius, OR, USA.

five-fold on wetting the 0–0.01 m depth samples from both stands to 60% of WHC, but had little effect over the 0.1–0.5 m depth. Net NO_3^-–N production also increased significantly ($P < 0.05$) in the wetted samples, except at 0.3–0.5 m depth in the old stand.

3.3. Carbon mineralization in laboratory-incubated samples before and after wetting

In the incubated litter from both stands, cumulative CO_2–C production was essentially linear at the field-sampled water content (Fig. 1). However, the respiration rates were extremely low and wetting to 60% of WHC corresponded with more than a 400-fold initial increase in CO_2–C production; rates gradually declined with time after 14 days. Over the 56-day incubation at 60% of WHC, 11 and 10% of total (initial) C was respired in samples from the young and old stand, respectively.

Although soil water content of the field-moist samples of mineral soil increased with depth in both stands ($P < 0.05$), the increase over 0.1–0.5 m depth was more marked in the old stand ($P < 0.10$, Table 1). In mineral soil at field-moisture content, cumulative CO_2–C production over 56 days was likewise higher, by about 1.6-fold, in the old- than in the young-stand samples (Fig. 2A–C); however, the rates were significantly higher only at 0–0.1 m depth, both in the field-moist samples and samples at 60% of WHC. Over the 56-day incubation, an average of 1.1 and 2.4% of total

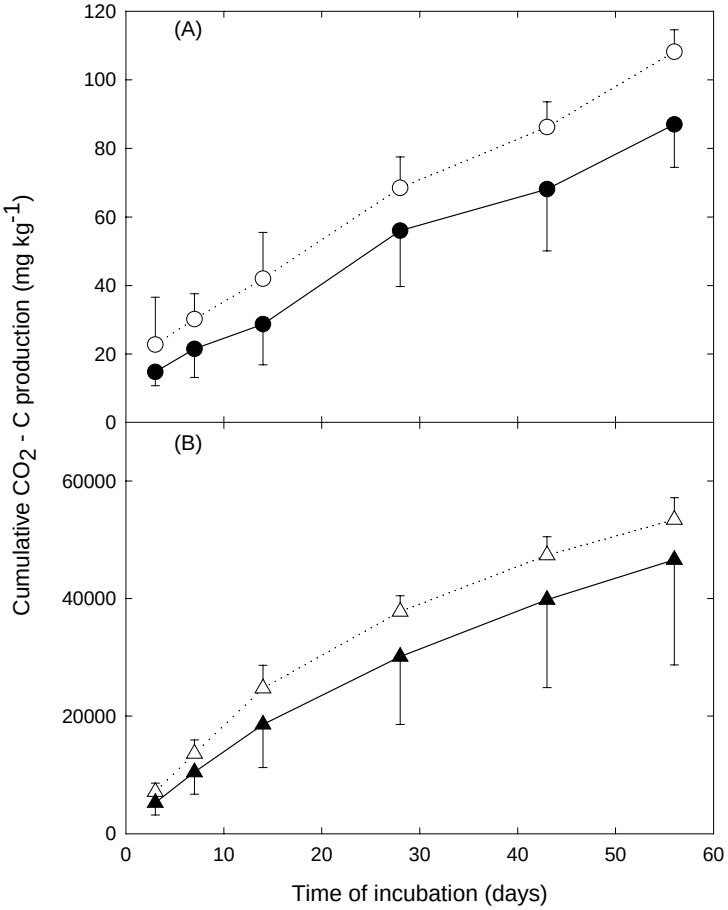

Fig. 1. Relations between cumulative CO_2–C production (mg kg^{-1} sample) at 25 °C and incubation time for litter from the young and old stands (open and closed symbols, respectively, represent averages) at field-sampled and wetted (60% of WHC) water contents (A and B, respectively); standard deviations are indicated by the error bars. Note the different scales on the *Y*-axis.

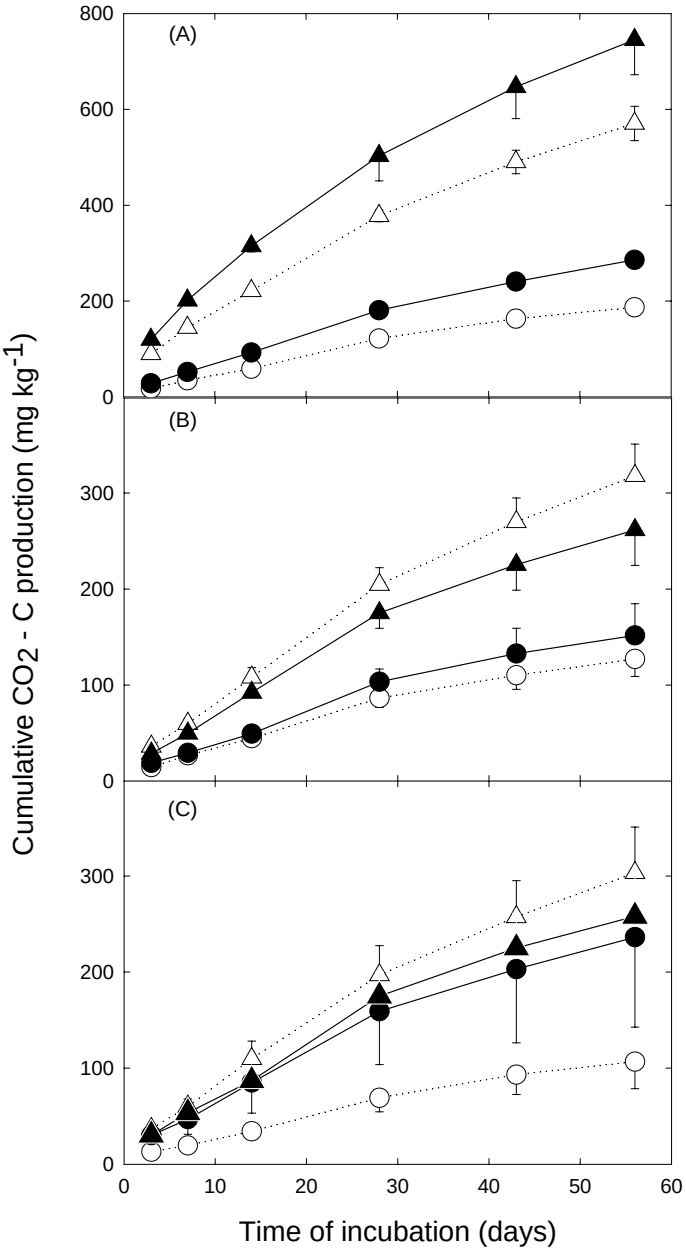

Fig. 2. Relations between cumulative CO_2–C production (mg kg^{-1} soil) at 25 °C and incubation time for mineral soil from the young and old stands (open and closed symbols, respectively, represent averages) at field-sampled and wetted (60% of WHC) water contents (circles and triangles, respectively) from depths 0–0.1 m (A), 0.1–0.3 m (B) and 0.3–0.5 m (C); standard deviations are indicated by the error bars. Note the different scales on the *Y*-axis.

(initial) C was respired by field-moist samples of mineral soil from the young and old stands, respectively; corresponding values for the samples at 60% of WHC were 3.1 and 3.6%.

Respiration rates (expressed on a total C basis) over 7–14 days were similar in the young- and old-stand samples at 60% of WHC (Table 3); these samples also had similar microbial C-to-total C and microbial N-to-

Table 3
Carbon dioxide (CO_2–C) production rates, on a total C basis, over days 7 to 14 during incubations at 25 °C of field-moist samples and samples wetted to 60% of water-holding capacity (WHC); also shown are ratios of CO_2–C production rate and water content (g kg^{-1} sample), the latter given in Table 1

Sample	CO_2–C production rate (mg kg^{-1} total C h^{-1})		CO_2–C production rate: water content ratio (mg kg^{-1} total C h^{-1}): (g kg^{-1} sample)	
	Field-moist	60% of WHC	Field-moist	60% of WHC
Young stand				
Litter	0.11 (0.03)	137 (17)	0.002	0.11
Mineral soil				
0–0.1 m	6.2 (1.8)	24 (2)	0.16	0.10
0.1–0.3 m	11 (1)	29 (3)	0.16	0.14
0.3–0.5 m	11 (3)	36 (7)	0.13	0.18
Old stand				
Litter	0.10 (0.02)	103 (33)	0.002	0.09
Mineral soil				
0–0.1 m	11 (1)	30 (5)	0.28	0.12
0.1–0.3 m	15 (1)	32 (2)	0.18	0.15
0.3–0.5 m	37 (17)	37 (5)	0.37	0.17

Values are means with standard deviations in parentheses. Litter and mineral soil were sampled on 25 July 2000 beneath two stands of *P. ponderosa*, Metolius, OR, USA.

total N ratios. An estimate of CO_2–C production on an area basis, based on the laboratory data, was made for the young stand using measured field temperature and bulk densities. The microbial respiration rate of litter plus mineral soil (0–0.5 m depth) was then calculated to be 1.1 μmol CO_2 m^{-2} s^{-1} (based on field-moist samples collected on 25 July; Table 4). For samples wetted to 60% of WHC, the corresponding microbial respiration rate was 4.5-fold higher at 5.0 μmol CO_2 m^{-2} s^{-1}. The CO_2–C production-to-water content ratio for our incubated samples was surprisingly robust at 0.1–0.2, except for the dry, field-moist, litter and the old-stand mineral soil samples from depths 0 to 0.1 and 0.3 to 0.5 m (Table 3).

Table 4
CO_2–C production rates over a 7–14-day incubation, as expressed on an area basis (μmol m^{-2} s^{-1}), of field-moist samples and samples wetted to 60% of WHC; field-moist and 60%-WHC water contents are given in Table 1

Sample	CO_2–C production rate (μmol m^{-2} s^{-1})			
	Field-moist		60% of WHC	
	At 25 °C	Adjusted to field temperatures	At 25 °C	Adjusted to field temperatures
Litter	0.002	0.002	2.2	1.8
Mineral soil				
0–0.1 m	0.4	0.3	1.5	1.2
0.1–0.3 m	0.7	0.5	1.8	1.1
0.3–0.5 m	0.6	0.3	1.9	0.9
Total	1.7	1.1	7.4	5.0

Litter and mineral soil were sampled on 25 July 2000 beneath a young stand of *P. ponderosa*, Metolius, OR, USA. Rates are given as measured at 25 °C, and after adjustments to measured field temperatures on 23 July 2000 (when soil water content was similar to the field-moist value on 25 July 2000) and 23 August 1999 (when soil water content was 60% of WHC) according to the Lloyd and Taylor (1994) model. On 23 July and 23 August, the field-measured CO_2–C production rates, including roots, at the soil surface were 1.6 and 4.0 μmol m^{-2} s^{-1}, respectively.

3.4. Relationships between carbon and nitrogen mineralization in laboratory-incubated samples

Carbon and N mineralization responses to the addition of water differed markedly in the Oregon litter samples, being 490- to 533-fold higher for cumulative CO_2–C production but only 2.3- to 5.0-fold higher for net min N production over the 56-day-long incubation. Responses to the addition of water were, however, roughly similar for cumulative CO_2–C production and net min-N production in the samples of mineral soil incubated for 56 days. The ratios of values at 60% of WHC to those at field-moisture content averaged 2.3 ± 0.8 for CO_2–C and 3.1 ± 2.3 for net min-N production, and generally showed no consistent trends at the different depths. The relationships between cumulative CO_2–C and net min-N production in 0–0.1 m depth mineral soil were, however, non-significant in field-moist samples ($P = 0.19$, $n = 4$) and in samples at 60% of WHC ($P = 0.37$, $n = 4$).

3.5. Soil respiration rate in the field during a summer drought and after wetting

On 7 July, before irrigation in the young stand at 1240–1330 h, soil respiration rate was not significantly different in the to-be-irrigated and control collars (1.5 ± 0.4 and 2.0 ± 0.8 μmol CO_2 m^{-2} s^{-1}, respectively, when soil temperatures at 0.15 m depth were 20.0 ± 1.5 and 18.0 ± 2.3 °C, respectively, $n = 5$, Fig. 3). The corresponding θ values at 0.1 and 0.3 m depths were 0.074 and 0.080 m^3 m^{-3} (average of 6 horizontal sensors at each depth), respectively. For the 0.3 m, deep root zone, soil water storage was thus 22.5 mm. Irrigation, from 1400 to 1500 h on 7 July, was 27 mm and there was also 1.8 mm rainfall at 1600 h so that, assuming no drainage, soil water storage became 51.3 mm or $\theta = 0.17$ m^3 m^{-3}. According to the soil water release curve, the matric potential ψ was thus −89 and −1 MPa before and after irrigation, respectively. The root zone can store 90 mm of water against gravity (i.e., $\theta = 0.3$ m^3 m^{-3} when $\psi = -0.005$ MPa), so irrigation achieved the equivalent of a 57% wetting of the soil.

At 1420–1450 h on 8 July, the soil respiration rate for the irrigated collars was significantly greater than for the controls ($P < 0.01$; 3.2 ± 1.2 versus 2.1 ± 0.6 μmol CO_2 m^{-2} s^{-1}, respectively, when soil temperatures were 21.0 ± 1.6 and 21.7 ± 1.4 °C, respectively; Fig. 3). Following irrigation, the soil respiration rate thus doubled in 1 day while there was no change in the control collars despite nearly

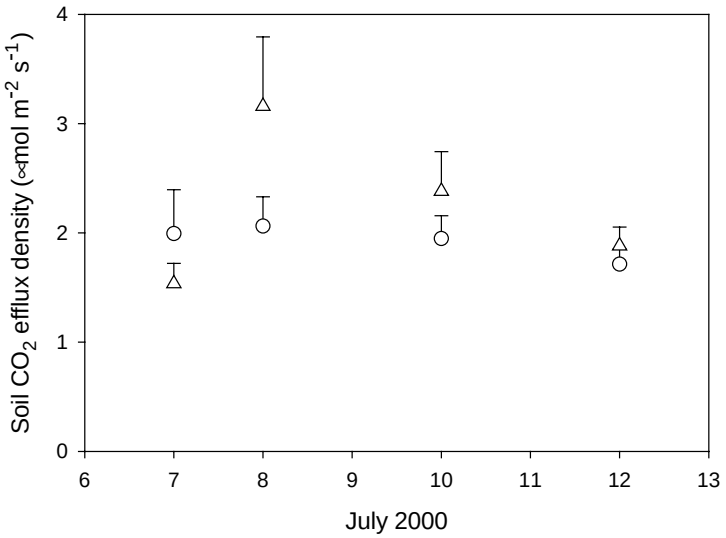

Fig. 3. Soil respiration rate in the young stand during a summer drought (circles) and after irrigation (triangles); standard deviations are indicated by the error bars. Collars were irrigated following soil respiration measurements on July 7 and July 10. Irrigation from 1400 to 1500 h on 7 July was 27 mm and was followed by 1.8 mm rainfall at 1600 h; assuming no drainage, soil water storage then became 51.3 mm or $\theta = 0.17$ m^3 m^{-3}. The second irrigation, equivalent to 34 mm rainfall, was applied at 1530 h on 10 July.

a 3 °C increase in soil temperature. The limitation of drought on soil respiration rate in the control collars is illustrated by noting how, under well-watered conditions, this temperature increase should correspond with a 30% increase in soil respiration rate according to Lloyd and Taylor (1994).

At 1440–1520 h on 10 July, soil respiration rate for the irrigated collars was not significantly greater than for the controls (2.4 ± 0.8 versus 1.9 ± 0.4 μmol CO_2 m^{-2} s^{-1}, respectively, (Fig. 3) when soil temperatures were 22.4 ± 1.5 and 23.9 ± 2.2 °C, respectively). For the 3 days following irrigation, air temperature and air-saturation deficit ranged from 9 to 22 °C and 0.2 to 2.2 kPa, respectively. Soil evaporation rate and θ were not measured in the irrigated collars. However, the energy-limited, equilibrium evaporation rate averaged 4 mm per day ($E_{eq} = [\varepsilon/\lambda(\varepsilon + 1)]R_a$, where ε, λ and R_a are, respectively, the rate of change of latent heat of saturated air with change of sensible heat content, latent heat of vaporization, and available energy flux density for the forest). Consequently, 3 days later, the surface soil dried to its pre-irrigation water content.

A second irrigation, equivalent to 34 mm rainfall, was applied at 1530 h on 10 July. At 0850–0930 h on 12 July, soil respiration rate for the irrigated collars was not significantly greater than the controls (1.9 ± 0.4 versus 1.7 ± 0.2 μmol CO_2 m^{-2} s^{-1}, respectively, (Fig. 3) when soil temperatures were 14.5 ± 0.7 and 14.8 ± 0.6 °C, respectively). This confirmed that the respiratory response of this sandy loam soil to irrigation was confined to a single day.

4. Discussion

The undisturbed old-growth and nearby young stands were chosen to determine if there was a difference in soil microbial activity associated with disturbance effects on substrate quantity and quality under similar climatic conditions. Because of the semi-arid climate, we also examined the limitation of water availability on microbial activity. Following the argument of Gulledge and Schimel (2000), this approach was adopted to elucidate processes that will govern soils associated with similar vegetation and climate.

The litter properties may be interpreted to suggest quantity of litter and dead fine roots was not significantly different between stands, but quality and decomposition rate were potentially higher in the young than in the old stand. We believe litter properties in the young stand were related mostly to the presence of understorey shrubs. Foliar nitrogen concentration (N_f) can be a regulating variable of a leaf's respiration rate and the N_f of bitterbrush, a nitrogen-fixing plant, was twice that of the pine (27.8 ± 1.1 versus 11.5 ± 0.5 mg g^{-1}), although the N_f values of manzanita and pine were indistinguishable (Law et al., 2001a). Moreover, potential litter decomposition rate can be inversely related to initial lignin concentration or the ratio of lignin-to-total N concentration (Melillo et al., 1982; Taylor et al., 1989). Foliar lignin concentration is postulated to reflect the concentration of non-labile substrates that can be decomposed by a few specialised fungi, but not by most bacteria (F.S. Chapin, personal communication). Lignin concentration was 35 and 40% in fresh pine needles from the young and old stand, respectively (Law et al., 2001b), whereas total N in litter was higher in samples from the young stand (Table 1). As ponderosa pine stands develop in this region, the N-fixing, understorey shrubs tend to decrease as a component of stand leaf area index (30% in the young stand to virtually nil in the old stand). Thus, as the young stand develops, litter quality would likely decrease.

Low net N mineralization in the litter of both stands on a total N basis (Table 2) probably reflects the predominance of L material in which net N immobilization greatly reduces or replaces net N mineralization (Ross et al., 2001). At 60% of WHC in the relatively decomposed lower layer of litter (FH layer) in two *Pinus radiata* plantations on sandy soils, net min-N production rate was much higher at 26 mg kg^{-1} total N h^{-1} (Ross et al., 1999b, 2001). In contrast, net N mineralization production rates at 25 °C in the mineral soil at 60% of WHC (Table 2) were similar, on a total N basis, to the values of 16 and ca. 17 mg kg^{-1} total N h^{-1}, respectively, in the 0–0.1 m depth samples from *P. radiata* (Ross et al., 1999b) and *Pinus sylvestris* (Priha and Smolander, 1997) forests. Litter decomposition rates were much greater in the laboratory, at 25 °C and 60% of WHC, than in the field where only 14 ± 1 and 18 ± 3% of the mass of pine-needle litter (equivalent to 7 and 9% of the litter C) was found to have respired from young- and old-stand samples, respectively, when the needles were exposed for a year in mesh bags on the soil surface (Law et al., 2001b). The comparable (percentage) litter mass loss

from 56-day-long laboratory and 365-day-long field studies illustrates limitations of the Oregon climate, with its long periods of relatively cold temperature and drought.

Overall, C mineralization appears to be at least as sensitive as net N mineralization to drought limitations in these Oregon forests. However, the non-significant relationships between cumulative CO_2–C production and net min-N production in 0–10 cm depth mineral soil differ from the significant relationships found by Parfitt et al. (2003) with samples taken from three adjacent ecosystems (indigenous forest, pasture and pine) on the same parent material. Our results also differ from those of Zak et al. (1999) who found, with 112-day incubations at 25 °C, that microbial respiration in 0–0.1 m depth samples of mineral soil from two deciduous forests in Michigan was somewhat more sensitive to dry conditions (1.5-fold higher for the wetter sample, analogous to our 60% of WHC sample) than was N mineralization (1.1-fold higher). There, the samples had been mixed with water to achieve matric potentials of −0.01 and −1.85 MPa.

Although microbial respiration rate in soil is usually limited by the availability of labile substrate, our data illustrate how soil water deficit can also be limiting. In a mixed deciduous forest, in Massachusetts, there was also a strong correlation between litter microbial activity and its water content (Borken et al., 2003). In Oregon, the soil is warmest during summer and microbial respiration should thus be highest if it were not for the effect of drought. Zak et al. (1999) concluded that the potentially high rates of microbial respiration at warm soil temperatures are limited by diffusion of substrate to metabolically active cells. For a given soil, diffusion rates depend mostly on water content. Because there would have been the highest possible gas diffusion rate in our field-moist (i.e., dry) samples, it may be that the limitation of summer drought on microbial respiration rate in the Oregon forests is separate from root respiration response. There were statistically separate, and identical, normalised sensitivites of soil (root and microbial) respiration rates to soil temperature and water content (expressed volumetrically, and multiplied by 100) in an 8-year-old ponderosa pine forest located 800 km south of the Oregon study site (Qi and Xu, 2001). We used the empirical model of Irvine and Law (2002) to separate the effects of temperature and soil water deficit on soil respiration, in the young stand only. The model is driven by daily averages of soil temperature and water content measured at depths of 0.15 and 0.10 m, respectively (see model 6 in Table 2 of Irvine and Law, 2002). We ran the model with measured data for the year 2000 when soil water content declined markedly during a typical summer drought, and for the same temperature data (a necessary assumption), but with soil water content set to 0.28 $m^3\ m^{-3}$ (nearly 60% of WHC) throughout the year. For the typically dry and hypothetically wet years, the model predicted annual soil respiration of 0.4 and 1.0 kg C m^{-2}, respectively. Soil water deficit during summer drought thus caused a 2.5-fold decrease in annual soil respiration rate, an encouraging result in agreement with those from our laboratory and field-soil wetting experiments.

5. Conclusions

Although the young stand had been harvested 22 years before sampling, its litter and mineral soil properties did not differ greatly from those of a relatively undisturbed, 250-year-old stand. However, concentrations of extractable and microbial C, and total, extractable organic and microbial N were higher in litter from the young stand, possibly because of the nitrogen-fixing broadleaf understorey species there. Net N mineralization, but not respiratory activity, in field-moist litter sampled during a summer drought was also greater in samples from the young stand. In both stands, net N mineralization of mineral soil from 0 to 0.1 m depth increased four- to five-fold upon wetting to 60% of WHC; water effects were mainly not significant at greater depths. Respiratory activity of the litter increased about 500-fold upon wetting to 60% of WHC; in mineral soil, the corresponding increase was two- to three-fold. The broadly conservative laboratory-based proportionality of soil respiration rate and water content was supported by field measurements of soil respiration in the young stand, before and after irrigation. A hypothetically wet year without soil water deficit caused a 2.5-fold increase in a modelled estimate of the young stand's annual soil respiration rate. In the semi-arid climate of central Oregon, microbial activity in litter and mineral soil beneath ponderosa pine forests would be limited more

by the availability of water in summer than by a lack of available C or N.

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