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Effects of temperature and moisture on carbon respired from decomposing woody roots

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Abstract

Controls of temperature and moisture on root decomposition have not been well studied despite their direct relevance to climate change impacts on root carbon flux. The main objective of this laboratory study was to examine the respiration response of Sitka spruce, Douglas-fir, western hemlock, ponderosa pine, and lodgepole pine decomposing roots (1–3 cm in diameter) to temperature and moisture change. Roots of Sitka spruce, Douglas-fir and western hemlock, and ponderosa pine and lodgepole pine were collected from Cascade Head, H.J. Andrews, and Pringle Falls site, respectively. Dead root respiration increased with temperature and reached the maximum at 30–40°C, and then decreased. Analysis of covariance indicated that the Q_{10} of root decomposition rate was influenced significantly ($p<0.01$) by incubation temperature range 5–40°C, but not by species, decay class or the direction of temperature change. At 5–10°C, Q_{10} averaged 3.99 and then decreased to 1.37 at 30–40°C. Over a range of 5–60°C, Q_{10} could be predicted by a single-exponential model using temperature as the independent variable. Analysis of variance showed that the respiration rate of dead roots was significantly ($p<0.01$) influenced by root moisture, species, and decay class as well as temperature. Dead root respiration increased with root moisture, reached the optimum range when moisture was between 100 and 275% and then decreased. Moreover, there were apparent interactions of root moisture and temperature on root respiration. Our study showed the direction of temperature and moisture change did not significantly influence root respiration, indicating that hysteresis may not occur for the temperature and moisture ranges examined. To better model global climate warming effects on root carbon flux, we suggest a temperature dependent Q_{10} function should be incorporated into current root dynamics models. The short-term laboratory incubation approach provided a good way to examine temperature and moisture controls on root decomposition, although we are cautious about long-term mass-loss extrapolations based on these short-term results.

Keywords: Roots; Respiration; Q_{10}; Global climate change; Hysteresis

1. Introduction

As researchers try to gain a better understanding of the possible impacts of global climate change on carbon and nutrient cycling in forest ecosystems and their feedback to climates, increasing attention is being focused on root dynamics belowground (Walker and Steffen, 1998). Root systems store large amounts of carbon and nutrients in forest ecosystems (Waid, 1974; Berg, 1984). More than 200 Mg ha^{-1} of root biomass has been estimated in old-growth coniferous forests of the Pacific Northwest of USA with 50–80% of these roots in the form of necromass (Vogt et al., 1986, 1991; Nadelhoffer and Raich, 1992; Ehrenfeld et al., 1997). Experimental studies have indicated that photosynthetic rate is generally

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increased for plants grown in elevated CO_2 environment (Strain, 1987; Gunderson and Wullschleger, 1994) and this leads to additional carbon to be allocated to roots (Norby et al., 1987). Meanwhile, elevated atmospheric CO_2 changes may lead to a warmer, moister future climate (Houghton et al., 1996), which in turn would generally enhance root decomposition in forest ecosystems. The future carbon store and nutrient balance of forest ecosystems strongly depend on the degree that increased decomposition of roots offset by increased production belowground.

Decomposition of roots, like other litters, is influenced by climatic environment as well as substrate quality and the decomposer community (Swift et al., 1979; Berg, 1984; McClaugherty et al., 1984, 1985; Heal et al., 1997). However, past studies on root decomposition have primarily focused on the influences of root substrate quality (Berg, 1984; McClaugherty et al., 1984; Fahey et al., 1988; Camire et al., 1991; Bloomfield et al., 1993), soil fauna, and soil type (Judas et al., 1995; Gijsman et al., 1997). Very few studies have dealt with the temperature and moisture controls on root decomposition (King et al., 1997). In contrast, the response to change of temperature, moisture, or both of aboveground litters is well known (Bartholomew and Norman, 1946; Witkamp and Van der Drift, 1961; Flanagan and Veum, 1974; Boddy, 1983; Moore, 1986; O'Connell, 1990). Experimental studies directly testing temperature and moisture controls on root decomposition, although few in number, are critical for developing a predictive understanding of root decomposition (Waid, 1974; Berg, 1984; Camire et al., 1991).

Past studies indicate that litter respiration generally increases with increasing temperature and moisture in certain range (Bartholomew and Norman, 1946; Witkamp and Van der Drift, 1961; Flanagan and Veum, 1974; Boddy, 1983; Moore, 1986; Taylor and Parkinson, 1988a, 1988b; O'Connell, 1990). The temperature responses of root respiration is frequently expressed as a Q_{10} function which indicates the change in respiration rate for a 10°C rise in temperature. The Q_{10} values of aboveground litters or soil organic matter appear to be higher in cold climate than in warm climatic regime (Schlesinger, 1977; Singh and Gutpka, 1977; Kirschbaum, 1995; Winckler et al., 1996). However, the effects of moisture, species, and decay class of dead roots on Q_{10} are simply unknown. Moreover, there are strong interactive effects of temperature and moisture on litter respiration (Flanagan and Veum, 1974; Bunnell et al., 1977; Boddy, 1983; Moore, 1986; O'Connell, 1990). Flanagan and Veum (1974) indicated that at lower moisture contents (<50% of dry weight) temperature increases had little effect on respiration of tundra litters, but at higher moisture contents (100–225%), respiration was more responsive to temperature changes. Similarly, they noted that moisture changes had little effect on litter respiration at lower temperatures (<5°C), while at higher temperature (10–15°C), respiration was more responsive to moisture changes. Too little or too much water inhibited or even stopped litter respiration due to matric limitation or oxygen diffusion limitation, respectively (Flanagan and Veum, 1974; Bunnell et al., 1977; Boddy, 1983). Does the respiration of decomposing roots respond similarly to changes of temperature and moisture as that of litters on forest floor?

In addition to temperature and moisture responses, the presence of hysteresis effects of temperature and moisture on respiration of decomposing roots have not been tested, although they would be highly relevant. The earliest description of hysteresis appeared in physics and indicates that the relationship of a physical property (Y) and variable (X) is not unique, but dependent on whether X is increasing or decreasing. A good physical example is equilibrium soil water content which depends on whether the soil is drying or wetting (Brady and Weil, 1996). All current decomposition models assume hysteresis effects of temperature and moisture on litter decomposition are minimal (Jenkinson et al., 1991; Raich et al., 1991; Potter et al., 1993; Raich and Potter, 1995), although this assumption has not been tested.

The objectives of this study were to: (1) examine the effects of temperature and moisture change on respiration of decomposing roots (1–3 cm in diameter) of Sitka spruce (*Picea sitchensis* (Bong) Carr), Douglas-fir (*Pseudotsuga menziensii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg), ponderosa pine (*Pinus ponderosa* Laws.), and lodgepole pine (*Pinus contorta* Dougl ex Loud.); (2) evaluate the possible interactions between temperature and moisture on root respiration; and (3) test for hysteresis effects of temperature and moisture on respiration of decomposing roots. Due to the complex covariance

between temperature and moisture occurring in field sites, a laboratory incubation approach in which temperature and moisture regimes could be manipulated was used.

2. Methods

2.1. Sites and sampling procedures

Decomposing woody roots of Sitka spruce, Douglas-fir, western hemlock, ponderosa pine, and lodgepole pine were collected from Sitka spruce, Douglas-fir, and ponderosa pine forests at Cascade Head Experimental Forests (CAH), H.J. Andrews Experimental Forests (HJA), and Pringle Fall Experimental Forests (PRF), respectively. CAH is located on the pacific coast near Otis, OR. The climate is maritime, with a mean annual temperature of 10°C and mean annual precipitation of 3420 mm. Soils are silt loams to silt clay loams derived from marine silt stones, moderately well drained, and high in organic matter and nitrogen. The dominant forest type is a mixture of western hemlock and Sitka spruce, although small stands dominated by Douglas-fir also occur (Franklin and Dyrness, 1973). HJA is located 80 km east of Eugene, OR, on the west slope of the Cascade Range. The climate is also maritime, with wet, relatively mild winters and dry, cool summers. Mean annual temperature is 8.5°C and mean annual precipitation is 2300 mm. Soils are deep, well-drained dystrochrepts; slope gradient ranges from 20 to 60%. The forests are dominated by Douglas-fir and western hemlock at low elevation (1050–1550 m) (Franklin and Dyrness, 1973). PRF is located 57 km southwest of Bend, OR; east of the Cascades. The climate is modified continental, with a mean annual temperature of 5.7°C and mean annual precipitation of 525 mm. Soils are coarse loamy sand derived from aerially deposited dacite pumice. Topography is rolling to gentle slopes. The dominant forest type is a mixture of ponderosa pine and lodgepole pine (Franklin and Dyrness, 1973).

Woody roots of Sitka spruce were taken from trees that were clear-cut 1, 12, and 20 years ago at CAH. Douglas-fir and western hemlocks were collected from trees cut 1, 15, and 20 years prior to sampling at HJA. Ponderosa pine and lodgepole pine were sampled from 3 stands which were clear-cut 2, 11, and 23 years ago at PRF. These root samples were subjectively assigned to decay class I, II, and III, respectively, after referring to the decay class system of logs (Harmon et al., 1986). Class I was the least decayed and had the most extensive bark cover with a decay age of 0–3 years. Class II of roots, a decay age of 3–15 years, had most bark cover and root wood started to decompose. Class III was very decayed with some root wood left and bark had started to fall off. The decay age of class III was at least 20 years in this study. Root samples were collected in July 1996 and May 1997. At each root collection, two stumps of each species were selected at each stand. After excavating the soil surrounding the roots, 20–40 cm long small root samples (1–3 cm in diameter) were removed using a handsaw, labeled and put into a plastic bag as soon as possible to prevent water loss. Root samples were stored in a cooler during transportation and in a 1–2°C walk-in cooler at Corvallis before laboratory incubation.

2.2. Incubation

Since our purpose was to understand the response of respiration of decomposing roots to temperature and moisture change, but not to measure the exact respiration rate of decomposing roots, thus short term (4 h) incubation of root samples was used. Roots collected from the three sites were cleared of surface soil first and then they were cut into 6 cm long segments. The wet weight of each segment was recorded and then each segment was tagged with a unique numbered aluminum tag indicating the species, decay class, and replication number. Each root sample was placed in the bottom of a Mason jar (Ball, Muncie, IN) with a headspace of 500 ml.

2.2.1. Temperature effects

Root samples collected in July 1996 were used to evaluate temperature effects on root respiration. Samples of known moisture content were incubated at different temperatures to examine temperature effects on root respiration. Thirty Mason jars with root samples were incubated at 0, 3, 5, 10, 15, 30, and 40°C for 4 h, respectively. For each type of root we had two replicates. Temperatures of individual roots were first increased from 0 to 40°C and then decreased over the same series to test for possible hysteresis effects. After

those incubations, the 30 samples were incubated at 50 and 60°C to examine the high temperature effects on root respiration. Therefore, temperature range for laboratory incubation was from 0 to 60°C. The incubation temperature gradient was created by a refrigerator from 0 to 40°C. Beyond 40°C, water baths of 50 and 60°C were used. Preliminary studies indicated that the oxygen inside a Mason jar was sufficient for the incubated root segment to respire 4 h at 30°C at a rate that was not inhibited due to lack of oxygen (Chen and Harmon, unpublished data). Moisture content of root sample did not change very much after each 4 h incubation (e.g. approximately 3.1–6.9% moisture was lost in each laboratory incubation). Here we simply regarded the root moisture content unchanged during the incubations.

2.2.2. Moisture effects

Root samples collected in May 1997 were used to examine the effects of moisture and possible interactions between moisture and temperature on root respiration. Root samples were wetted or air-dried to generate a moisture gradient ranging from water saturation to very dry. All incubated roots were started at highest moisture content (230–300%) by soaking in water for 5 days and then dried to the lowest content (30–45%) and then rewetted to known moisture contents (60–120, 120–180, and 230–300%) until water saturation was reached. This design allowed us to test for hysteresis effects. At each moisture level, the root samples were incubated at 5, 15, and 30°C to evaluate the interaction between temperature and moisture on respiration. For each type of root we had two replicates.

2.2.3. Carbon efflux

Increases of CO_2 concentrations in Mason jars were measured by gas chromatography (HP 5890 Series II) after each incubation. The gas chromatograph (GC) used a He carrier and a thermal conductivity detector (TCD). At least a 45 min period was used for the TCD to warm up and stabilize. A standard using the 0.99% CO_2 gas was used and the GC was recalibrated if the standard CO_2 differed more than 0.05%. Pre-incubation of Mason jars was required at the incubation temperature for 1 h before 0.5 ml of air inside a Mason jar was sampled using a syringe and measured by GC as the time zero value. Four hours later, another 0.5 ml air sample was injected and measured similarly. The net increase of CO_2 concentration during the 4 h incubation at the temperature was used to calculate the respiration rate of the root. After all the required incubations were finished the root samples in Mason jars were oven-dried (65°C) for a week and the oven-dry weight (ODW) recorded. The initial moisture content of the root sample was calculated using the initial wet weight and ODW. The respiration rate k (μg carbon per gram dry-root per hour) of decomposing root was calculated from the formula:

$$k = \frac{\Delta CO_2}{100}\frac{1}{ODW}\frac{1}{IP} \times V \times 41.0339 \times 12 \quad (1)$$

where ΔCO_2 is the net percent increase of CO_2 concentration during the incubation period, ODW of root sample (g), IP the incubation period (h), V the net volume of headspace (500 ml — volume of root sample), 41.0339 the constant for converting CO_2 molar volume (ml) to micro mol at 25.9°C laboratory temperature and 1 atm pressure condition, and finally the whole formula is multiplied by 12 to convert micro mol of CO_2 to microgram of carbon.

The Q_{10} of respiration rate of decomposing roots in this study is calculated from the formula:

$$Q_{10} = \left(\frac{k_2}{k_1}\right)^{[10/(T_2-T_1)]} \quad (2)$$

where k_2 and k_1 are the respiration rates of decomposing roots incubated at temperatures T_2 and T_1 in °C, respectively.

2.3. Data standardization and statistical analysis

Respiration rates of decomposing roots at different incubated temperatures and moisture were first standardized either for each species or for all species combined to reduce the confounding influences of decay classes and/or species in evaluating temperature and moisture effects on root respiration. In the analysis of temperature effects, we standardized the respiration rates of roots based on each species and all species combined. For each species, the relative respiration rate of roots was the ratio of respiration rate and the maximum respiration rate for the entire range of incubation temperatures. Similarly, the relative respiration rate of all species at a temperature was the ratio of mean respiration rate of all species at that

temperature and the maximum mean respiration rate of the five species over the entire range of incubation temperatures. In the analysis of moisture effects, similar data standardization was conducted for each species based on three different incubation temperatures. Consequently, relative respiration rate of roots was always smaller than or equal to one.

Analysis of covariance (ANCOVA) was used to test the effects of temperature range, species, decay class, and direction of temperature change on the Q_{10} of respiration rate of incubated roots. Root moisture was treated as a covariance in this analysis. Two-way analysis of variance (ANOVA) was used to test how moisture, temperature, species, and decay class control root respiration. Differences between means were detected using Fisher's protected least significant difference (LSD). All statistical tests were performed by procedure GLM of SAS Institute (1985). Statistical tests were judged significant if $0.05>p>0.01$ and highly significant if $p\leq 0.01$.

3. Results

3.1. Temperature effect

The five different species responded to temperature change similarly with the relative respiration rate of roots increasing with incubation temperature, reaching a maximum at 40°C, and then decreasing above that temperature (Fig. 1).[1] The only exception to this pattern was lodgepole pine roots which reached a maximum at 30°C (Fig. 1e). Combining all the species, the relative respiration rate of roots reached a maximum at 40°C (Fig. 1a).

3.2. Factors influencing Q_{10}

ANCOVA indicated that the Q_{10} of root respiration rate was influenced to a highly significant degree ($p<0.01$) by the incubation temperature range 5–40°C, but not by species, decay class, or the direction of temperature change (Table 1). No significant impact of root moisture, a covariant in the analysis, was observed on the Q_{10} of woody roots. The Q_{10} of root respiration rate decreased with increasing temperature of incubation (Fig. 2).[2] For example, at 5–10°C, Q_{10} averaged 3.99, decreased to 2.4 at 10–15°C, and then further declined with increasing temperature. The Q_{10} of respiration rate of decomposing roots in the temperature range 5–10 and 10–30°C were significantly higher than those of the rest of the temperate ranges (Table 2). Regression analysis indicated that Q_{10} of root respiration rate could be expressed by single-exponential model:

$$Q_{10} = 4.31e^{-0.036\text{Temp}}$$

where Temp was temperature (°C). This model was significant ($p<0.02$) and accounted for 77% of the variation of Q_{10}.

The direction of temperature change did not significantly influence Q_{10} of root respiration rate ($p=0.54$), indicating that hysteresis may not occur for the examined temperature range 5–40°C (Tables 1 and 2). However, the standard errors of Q_{10} were large in comparison to the mean Q_{10} values, especially on low incubation temperature such as 5–10°C range (Table 2), suggesting better experimental design using more tightly constrained decomposing roots would be needed in future to detect whether hysteresis really occurs or not with the direction of temperature change in root decomposition.

3.3. Moisture effects

The relative respiration rate of roots increased with root moisture, reached a peak at an optimum moisture range, then decreased beyond that moisture, regardless of incubation temperatures (Fig. 3).[3] The exceptions to this pattern were Douglas-fir, ponderosa pine, Sitka spruce which continuously increased with increasing moisture. The optimum root moisture differed among species. For example, the optimum moisture range of

[1] For individual species, number of replications of the mean are $n=12$ in the temperature range 0–40°C and $n=6$ in temperature range 50–60°C. For all species combined, the replications are $n=60$ in temperature range 0–40°C and $n=30$ in the temperature range of 50–60°C.

[2] Q_{10} value was calculated from 60 replications in each incubation temperature range lower than 40°C. Beyond 40°C, each mean Q_{10} was calculated from 30 replications. Different letters indicate significant difference among the means ($p<0.05$).

[3] For the respiration rate in Figs. 3 and 4, each mean was calculated from two replications of three decay class root samples.

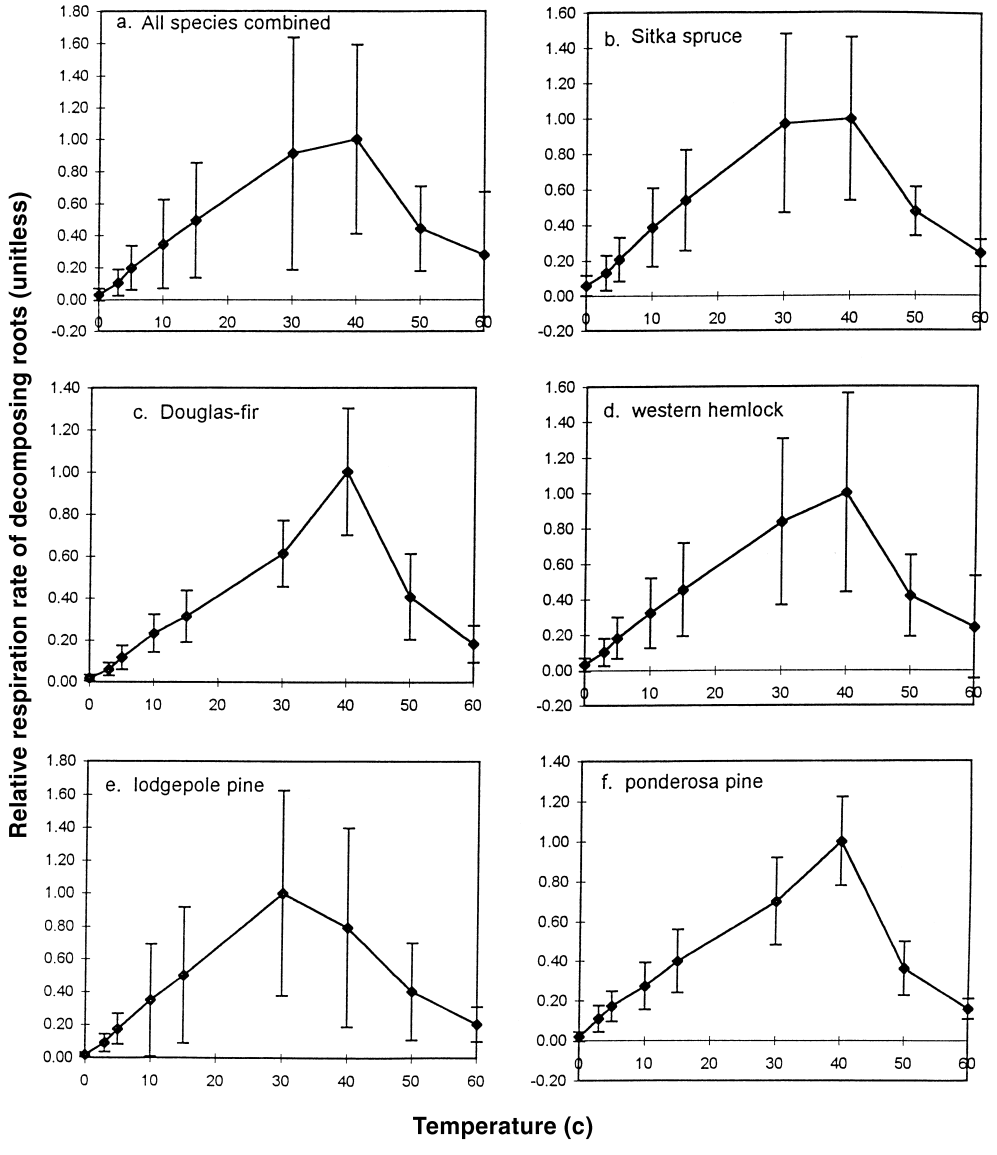

Fig. 1. Relative respiration of decomposing roots incubated 4 h at different temperatures: (a) All species combined, (b) Sitka spruce, (c) Douglas-fir, (d) western hemlock, (e) lodgepole pine, and (f) ponderosa pine. Solid bars denote means of relative respiration rates (+S.E.).

lodgepole pine was between 125 and 225%. While the optimum moisture of Sitka spruce was wider, at least ranging from 125 to 275%, although we were not sure what would happen to the relative respiration rate when moisture was higher than 275%. When the moisture of woody roots was reduced to 20–50%, the relative respiration rate was very low for all five species examined.

Two-way ANOVA indicated that the respiration rate of decomposing roots was highly significantly influenced by root moisture and incubation temperature ($p<0.01$), but not by the direction of moisture change ($p=0.14$). The interaction of temperature and moisture on root respiration rate was also highly significant ($p<0.01$) (Table 3 and Fig. 4). At a very low root moisture content, the effects of three different incuba-

Table 1
ANCOVA results of factors influencing the Q_{10} of respiration rate of decomposing roots

Source	d.f.	Sum of squares	Mean square	F value	p value
Temperature	3,239	258.45	86.15	16.58	0.01
Species	4,239	25.00	6.25	1.20	0.31
Decay class	2,239	8.31	4.16	0.80	0.45
Direction	1,239	1.92	1.92	0.37	0.54
Moisture (covariate)	1,239	1.00	1.76	0.34	0.56

Table 2
Impact of the direction of temperature change on the Q_{10} of respiration rate of decomposing roots[a]

Direction	Temperature range (°C)			
	5–10	10–15	15–30	30–40
Increase	3.70 (3.63)	2.18 (1.14)	2.10 (0.30)	1.40 (0.68)
Decrease	4.30 (5.12)	2.62 (1.36)	1.90 (1.25)	1.33 (0.68)
Mean	3.99 (4.34)	2.40 (1.24)	2.02 (0.58)	1.37 (0.68)

[a] The value in parenthesis was one S.E.

tion temperatures were negligible, resulting in a very low respiration rate. Surprisingly the temperature effects from 5 to 15°C observed in the moisture experiment were not similar to those which occurred in the temperature experiment. In contrast, the responses of root respiration rate at 30°C was consistent with the temperature experiment (Fig. 4). The lack of influence of direction of root moisture change suggests that hysteresis effects did not occur.

3.4. Species and decay class effects

In addition to root moisture and incubation temperature, the respiration rate of decomposing roots was also highly significantly influenced by species and decay class ($p<0.01$) (Table 3). Among the five species examined, lodgepole pine showed the highest respiration rate with a mean value of 17.2 μg g^{-1} h^{-1}, western hemlock the second with a rate of 13.2 μg g^{-1} h^{-1}, and Douglas-fir, ponderosa pine, and Sitka spruce were similar, ranging from 6.3 to

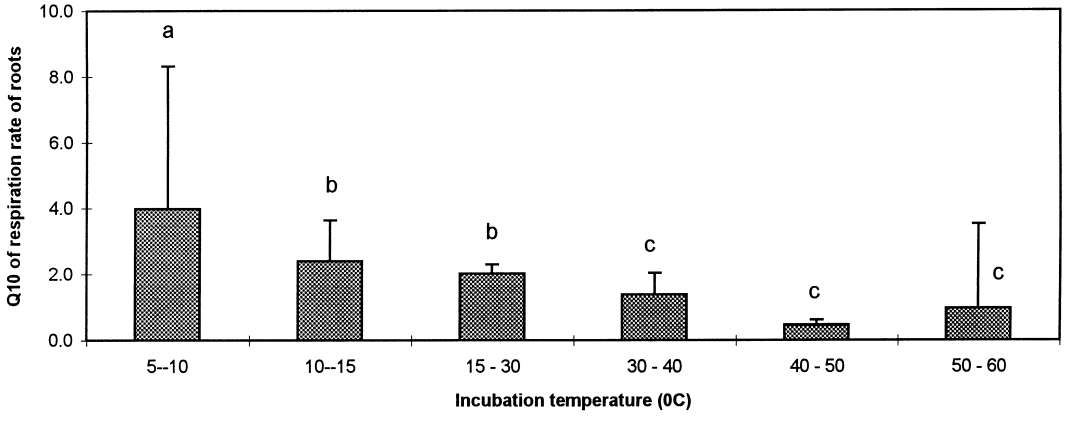

Fig. 2. Q_{10} for different ranges of incubation temperature. Solid bars denote means of Q_{10} (+S.E.).

Table 3
ANOVA results of the factors influencing respiration rate of decomposing roots

Source	d.f.	Sum of squares	Mean square	F value	p value
Moisture	5,749	12985.04	2597.01	25.89	0.01
Temperature	2,749	28442.29	14221.15	141.77	0.01
Moisture×Temperature	8,749	2131.04	266.38	2.66	0.01
Species	4,749	13260.46	3315.12	33.05	0.01
Decay class	2,749	2900.11	1450.05	14.46	0.01
Direction	1,749	216.09	216.09	2.15	0.14

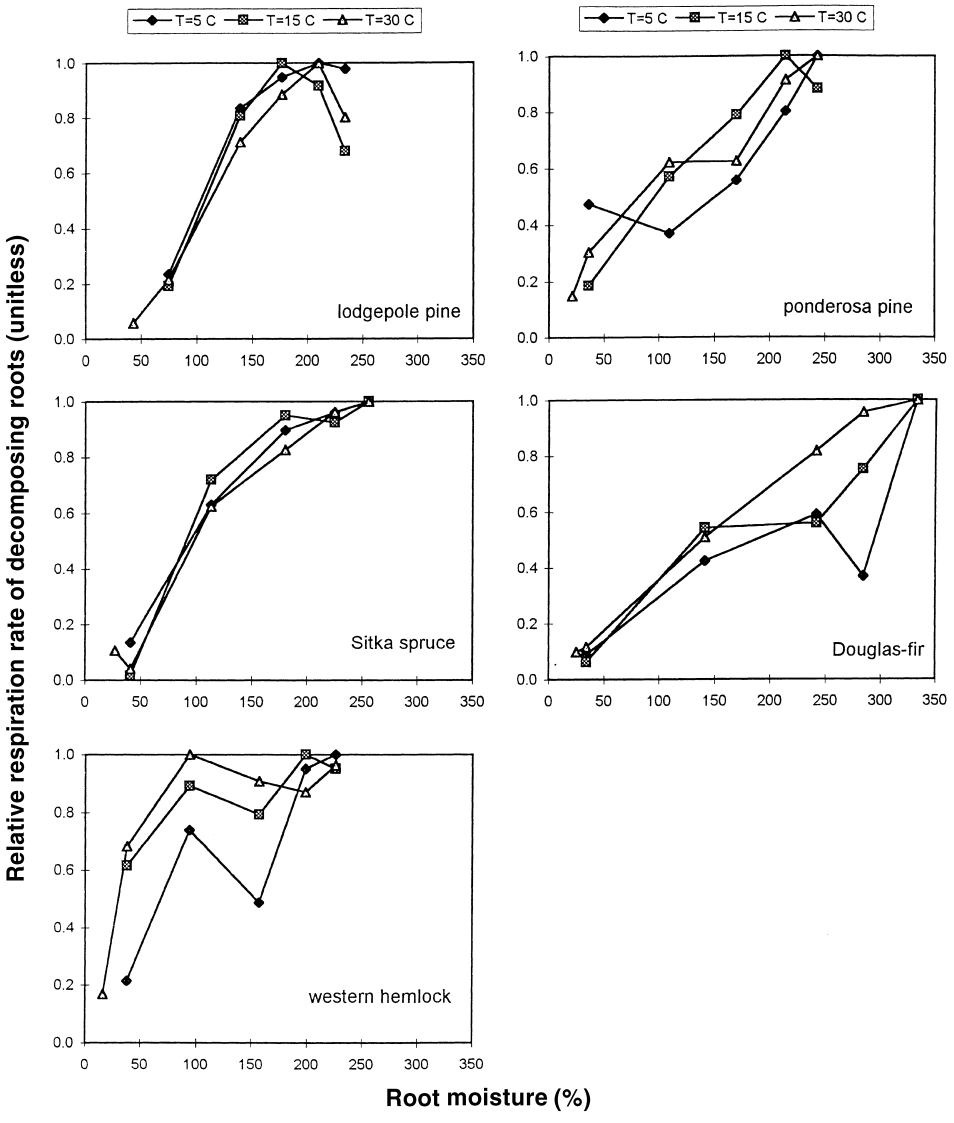

Fig. 3. Relative respiration rate of decomposing roots under different moisture and temperatures.

8.4 μg g^{-1} h^{-1} (Fig. 5).[4] Roots of decay class I and III had a significantly higher respiration rate than that of decay class II (Fig. 6).[5] The high standard error of respiration rate in Figs. 5 and 6 was mainly due to the fact that we had three temperature (5, 15, and 30°C) treatments in this experiment.

[4] Each mean value was calculated from 144 replications which include three decay class root samples. Different letters indicate significant difference among the means ($p<0.05$).

[5] Each mean was calculated from 270 replications which include root samples of Sitka spruce, Douglas-fir, western hemlock, lodgepole pine, and ponderosa pine. Different letters indicate significant difference among the means ($p<0.05$).

4. Discussion

4.1. Temperature effects

The general response of respiration of decomposing woody roots to temperature was very similar to those

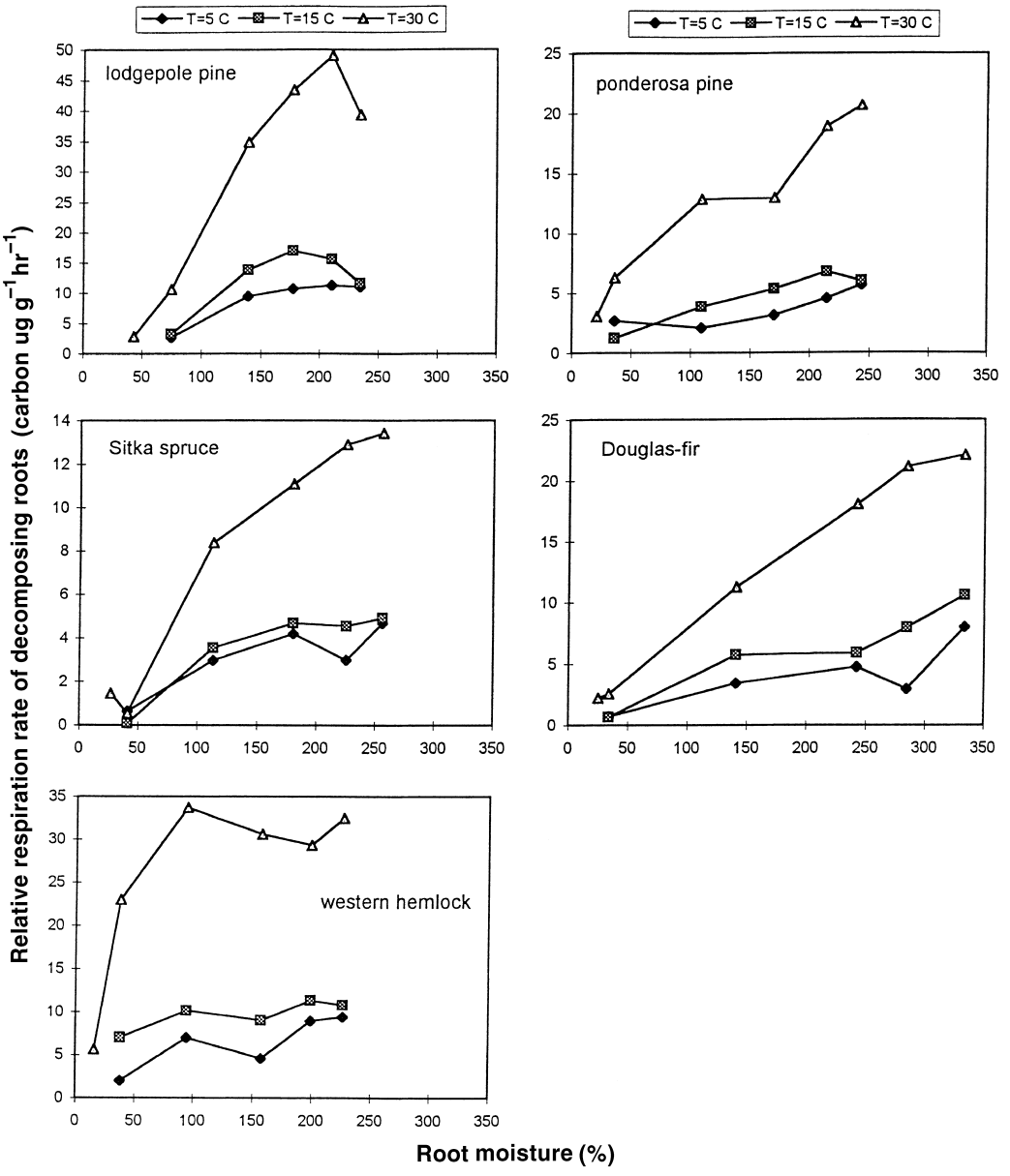

Fig. 4. Respiration rate of decomposing roots under different moisture and temperatures.

of aboveground litter: enhanced respiration with increasing temperatures up to an optimum temperature, and retarded respiration with temperature above that point (Flanagan and Veum, 1974; Boddy, 1983; Moore, 1986; O'Connell, 1990). Increasing temperature enhances the enzyme activities and hence respiration and enzymatic breakdown of polymers (McClaugherty and Links, 1990). The increase in of incubation temperature to 50 and 60°C caused the respiration of roots to decline (Fig. 1), although the respiration process did not stop completely. This decrease is probably due to the denaturing of decomposer protein. These high temperatures may occur in clear-cut forest sites where high radiation inputs occur.

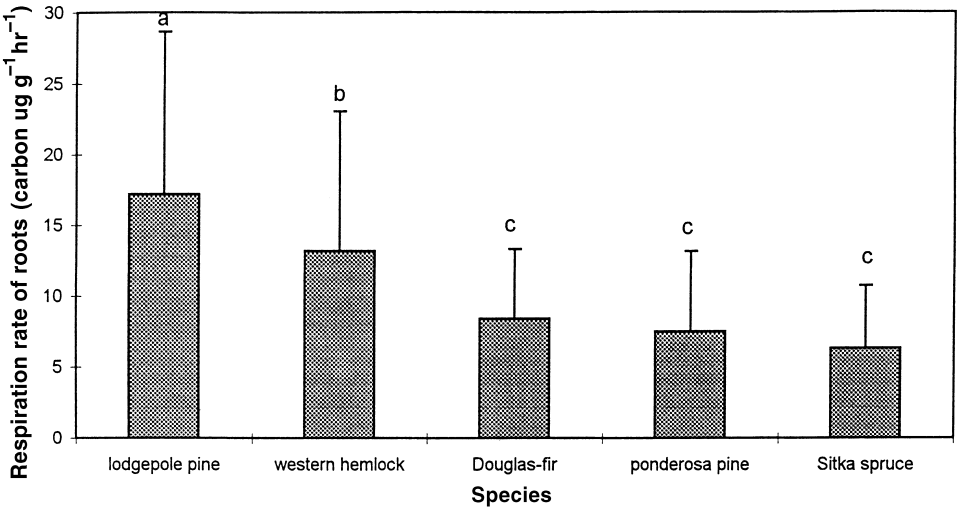

Fig. 5. Species effects on respiration rate of decomposing woody roots. Solid bars denote means of respiration rate (+S.E.).

In our study, the optimum temperature was between 30 and 40°C (Fig. 1), which is consistent with the incubation results of deciduous forest-leaf and Douglas-fir fine litter (Moore, 1986) and litter of eucalyptus forests at Australia (O'Connell, 1990). Moore (1986) indicated the decomposition rates of deciduous forest leaf sampled at North Carolina and Douglas-fir needles collected at HJA approached a maximum near 40°C. Similarly, O'Connell (1990) found that the optimum temperature for respiration of litter of eucalyptus forests was 33–34°C. However, Flanagan and Veum (1974) found that the optimum temperature of organic residues from the Alaska Tundra was 25°C. This low optimum temperature may be due to the decomposers of this Tundra region which might be adapted to cold climate. The similarity of temperature responses in temperate forests regardless of sampling season and site (this study and Moore, 1986) may

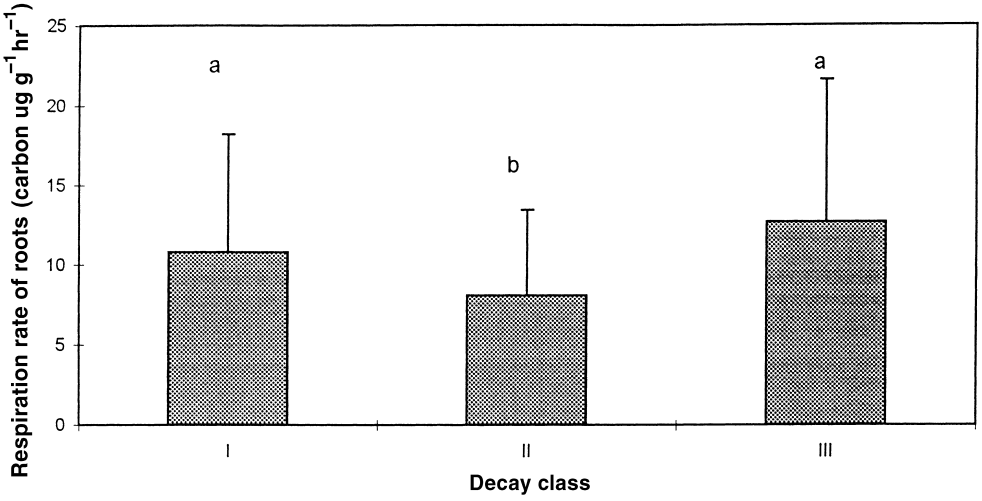

Fig. 6. Decay class effects on respiration rate of decomposing roots. Solid bars denote means of respiration rate (+S.E.).

indicate that the decomposer groups from the same climatic zone may be similar. Our preliminary laboratory incubation of decomposing root samples collected in the spring of 1996 from the same three stands at each site also showed an optimum temperature between 30 and 40°C (Chen and Harmon, unpublished data).

The Q_{10} of respiration rate of decomposing roots was significantly influenced by temperature being greater at low (Q_{10}=3.99, 5–10°C) than at moderate (Q_{10}=2–2.4, 10–30°C) or high (Q_{10}=0.46–1.37, 30–60°C) temperature (Fig. 2). The high Q_{10} values at low temperature indicate positive temperature effects on enzyme activities. In contrast, the low Q_{10} value at high temperature is due to increased enzyme denaturing. The Q_{10} pattern of decomposing roots was similar to those of soil organic matter (De Jong et al., 1974; Raich and Schlesinger, 1992; Kirschbaum, 1995; Winckler et al., 1996). Kirschbaum (1995) indicated that Q_{10} of soil organic matter decreased from almost 8 at 0°C to about 4.5 at 10°C and 2.5 at 20°C. Winckler et al. (1996) calculated that Q_{10} of A horizon soil of a temperate forest at North Carolina varied from 1.9 to 1.7 over the temperature range 4–28°C. Raich and Schlesinger (1992) compiled literature values from year round field studies and calculated an average Q_{10} of 2.4. Q_{10} values between 1.6 and 3.7 have been recorded for microbial respiration for many temperate and tropical systems over a temperature range between 10 and 40°C (Schlesinger, 1977; Singh and Gutpka, 1977; Anderson, 1992).

Species, decay class, and moisture of dead roots did not show a significant influence on Q_{10} as we had expected. We would expect that species with higher substrate quality should be more responsive to changes in temperature. This suggests that the relative activities of root decomposer be influenced more by abiotic factor such as temperature than biotic factors such as species and decay class. The lack of significant moisture effect on Q_{10} observed in this study is mainly due to the fact that most moisture contents of the samples incubated were between 100 and 240%, a moisture range favorable for microbial respiration.

4.2. Moisture effects

Both extremely low and high moisture contents can limit the activity of decomposer organisms. In our study, below 30% moisture content (the fiber saturation point), water was generally not available for metabolic activity of microbes. This result is similar to the other studies (Griffin, 1977; Boddy, 1983). Increasing moisture content enhanced respiration of roots until an optimum moisture range was reached. This optimum moisture content ranged between 100 and 275% depending on the species in our study. When root moisture was above the optimum range excess moisture probably retarded decomposition by reducing the diffusion rate of oxygen (Killham, 1994). High moisture limitation on root respiration was not observed in Sitka spruce, Douglas-fir and ponderosa pine (Fig. 3). This may be due to lack of water saturation in these species. A soaking period of more than 5 days may be needed to create their saturated moisture contents.

The interaction of temperature and moisture on respiration of dead roots differed depending on the moisture content of woody roots (Fig. 4). At low moisture contents (<75% of dry weight), temperature increases had little effect on respiration, but at higher moisture contents (100–200%), respiration was more responsive to temperature increases, especially in temperature range 15–30°C. Our results were very similar to those of Schlenter and Van Cleve (1985), who examined abiotic controls on soil respiration.

4.3. Short-term incubation versus long-term decomposition

Our main purpose in this study was to understand how the change of temperature and moisture influence the response of respiration of decomposing roots, but not to aim at measuring the exact respiration rate of decomposing roots. Qualitatively, root respiration was significantly influenced by species, decay class, root moisture, and incubation temperature observed in this short-term laboratory incubation study (Table 3), which is consistent with the results of most field root decomposition studies (McClaugherty et al., 1984; Fahey et al., 1988; Camire et al., 1991). However, we are cautious about long-term mass-loss extrapolations based on these short-term laboratory incubation results. Long-term root decomposition study in field sites is necessary to validate our respiration data. Nevertheless, the short-term laboratory incubation approach provided a good way to examine factors

controlling root decomposition and how these factors vary across their range in a relative sense.

4.4. Implications for global climate change modeling on root carbon flux

Soils are of particular importance in the atmospheric CO_2 budget. Soil organic matter contains a large reservoir of carbon, recently estimated at ~1600 Pg, more than twice the atmospheric carbon pool (Jenkinson et al., 1991; Raich and Potter, 1995). Dead roots are an important carbon pool in soil, accounting for up to one-third of total soil respiration in temperate soils (Bowden et al., 1993). Therefore an increase in the CO_2 flux from this pool in response to global climate warming will have a major influence on atmospheric CO_2 concentrations. A simple constant of $Q_{10}=2$ has been widely used in modeling temperature effects on carbon release from soil organic matter and other organic detritus, regardless of temperature conditions (Raich et al., 1991; Potter et al., 1993). Our study indicated that Q_{10} of respiration rate of decomposing roots decreased exponentially with increasing temperature. Similar changes in Q_{10} with temperature were observed in several soil organic matter studies (De Jong et al., 1974; Schlenter and Van Cleve, 1985; Kirschbaum, 1995; Winckler et al., 1996). A simple example illustrates the importance of using an appropriate Q_{10}. Assuming the annual temperature at PRF increases due to global climate warming to 10.7°C from a current mean temperature of 5.7°C, the carbon flux of dead roots will double if the Q_{10} of 4 (based on our laboratory study result) is used. In contrast, if the traditional Q_{10} of 2 is used the carbon flux of dead will increase only 1.4-fold. Therefore varying the Q_{10} between 2 and 4 would result in a 60% difference in the carbon flux from roots. The modeling of climate warming effects on forest root carbon flux should be considered to use a temperature dependent Q_{10} value in their models.

5. Conclusions

The respiration of dead roots increased with temperature and reached the maximum at 30–40°C, and then decreased. The Q_{10} of respiration rate of dead roots was significantly influenced ($p<0.01$) by temperature, but not by species, decay class, and the direction of change. At 5–10°C, Q_{10} averaged 3.99 and then decreased to 1.37 at 30–40°C. Over a range of 5–60°C, Q_{10} could be predicted by a single-exponential model using temperature as the independent variable. The respiration rate of decomposing roots was influenced to a highly significant degree by root moisture, species, and decay class. The optimum root moisture ranged from 100 to 275% depending on the species. When roots were too dry (<50%) or too wet (>300%), root moisture became a limiting factor. Moreover, there were apparent interactions of root moisture and temperature on root respiration. Our study showed that the direction of temperature and moisture change did not influence root respiration, indicating that hysteresis may not occur for either the temperature or the moisture ranges examined. The modeling of global climate warming effects on forest root carbon flux should consider a temperature dependent Q_{10} value. The short-term laboratory incubation approach provided a good way to examine temperature and moisture controls on root decomposition, although we are cautious about long-term mass-loss extrapolations based on these short-term results.

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