

Research review

Responses of tree fine roots to temperature

KURT S. PREGITZER*, JOHN S. KING, ANDREW J. BURTON
AND SHANNON E. BROWN

*School of Forestry and Wood Products, Michigan Technological University,
1400 Townsend Drive, Houghton, MI 49931, USA*

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SUMMARY

Soil temperature can influence the functioning of roots in many ways. If soil moisture and nutrient availability are adequate, rates of root length extension and root mortality increase with increasing soil temperature, at least up to an optimal temperature for root growth, which seems to vary among taxa. Root growth and root mortality are highly seasonal in perennial plants, with a flush of growth in spring and significant mortality in the fall. At present we do not understand whether root growth phenology responds to the same temperature cues that are known to control shoot growth. We also do not understand whether the flush of root growth in the spring depends on the utilization of stored nonstructural carbohydrates, or if it is fueled by current photosynthate. Root respiration increases exponentially with temperature, but Q_{10} values range widely from *c.* 1.5 to >3.0. Significant questions yet to be resolved are: whether rates of root respiration acclimate to soil temperature, and what mechanisms control acclimation if it occurs. Limited data suggest that fine roots depend heavily on the import of new carbon (C) from the canopy during the growing season. We hypothesize that root growth and root respiration are tightly linked to whole-canopy assimilation through complex source–sink relationships within the plant. Our understanding of how the whole plant responds to dynamic changes in soil temperature, moisture and nutrient availability is poor, even though it is well known that multiple growth-limiting resources change simultaneously through time during a typical growing season. We review the interactions between soil temperature and other growth-limiting factors to illustrate how simple generalizations about temperature and root functioning can be misleading.

Key words: roots, temperature, respiration, carbon, nutrients, water, atmospheric CO₂.

INTRODUCTION

Soil temperature can influence root growth, including the initiation and cessation of growth, cell elongation, root length and diameter extension, initiation of new lateral roots, and root branching patterns (Kasper & Bland, 1992; McMichael & Burke, 1998). Warmer soil temperatures often result in higher rates of root respiration and ion uptake if other factors, such as light and drought, do not limit the physiological activity of plants (Oertli, 1996; Burton *et al.*, 1998; BassiriRad, 2000). Rates of root mortality also seem to increase with soil temperature (Forbes *et al.*, 1997; King *et al.*, 1999), and the flux of C from plant roots into the soil foodweb might increase if global temperatures rise as predicted (Houghton *et al.*, 1996).

Changes in soil temperature interact with changes in other essential resources. For example, both water and nutrient availability often covary with changes in soil temperature. Higher soil temperatures result in increased nitrogen (N) mineralization if soil water potential does not limit microbial activity (Piatek & Allen, 1999; Zak *et al.*, 1999). However, drought conditions often occur when soil temperatures are relatively high (Kuhns *et al.*, 1985; Piatek & Allen, 1999). Interpretation of root–soil–temperature responses are complicated by these types of environmental interaction. Furthermore, soil temperature can affect photosynthesis, and as soil temperatures and photosynthesis increase together, changes in whole-plant source–sink relationships can occur (Lippu & Puttonen, 1991; Landhausser *et al.*, 1996). For example, low soil temperatures can limit rates of enzymically driven root processes such as growth, nutrient uptake, and respiration, decreasing the demand for C and resulting in a negative

*Author for correspondence (tel +1 906 487 2396; fax +1 906 487 2915; e-mail kspregit@mtu.edu).

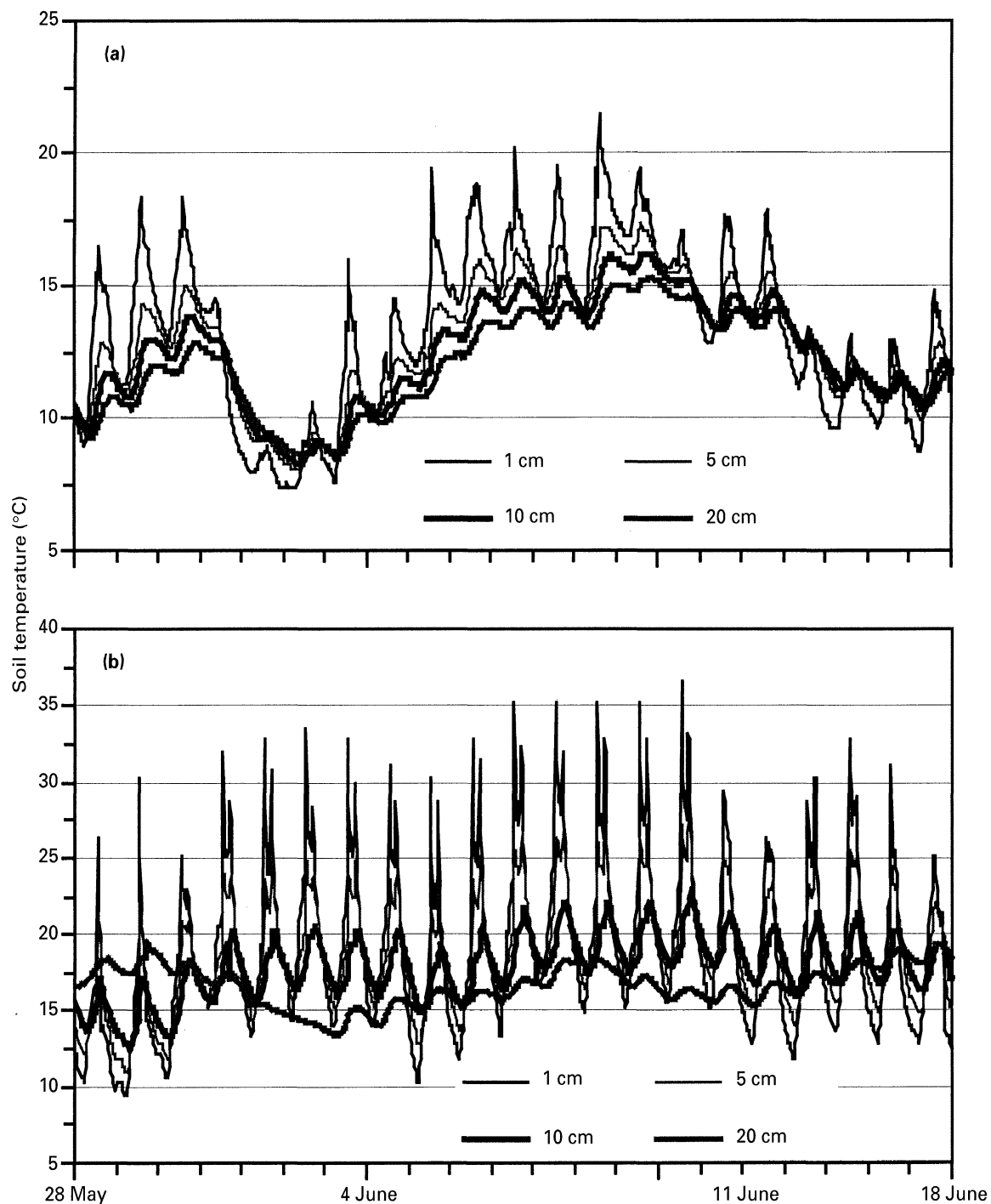


Fig. 1. Soil temperature profiles in a Michigan northern hardwood forest dominated by sugar maple (a) and beneath individual juniper trees in an open pinyon–juniper woodland (b) at the Sevilleta long-term ecological research (LTER) site in New Mexico, USA. Soil temperatures for the period 28 May to 18 June 1999 were recorded every 30 min with HOBO H-8 dataloggers (Onset Computer Corporation, Bourne, MA, USA).

feedback to photosynthesis through the accumulation of nonstructural carbohydrates in leaves (Thomas & Strain, 1991).

The search for generalizations about how soil temperature regulates root functioning must be tempered by the realization that different populations of plants have evolved to cope with a wide range of field temperature regimes. We know that temperature has an important role in regulating aboveground physiology and there are obvious questions that need to be addressed belowground at various taxonomic levels: life form, genus, species, and genotype. Finally, the age (ontogeny) of a plant

can also influence responses of roots to changing soil temperatures. Young perennial plants invest relatively more C in tissue construction, whereas older plants allocate a greater proportion of their annual C budget to the maintenance of the root system and the replacement of short-lived feeder roots. We should be careful of generalizations derived from laboratory experiments that can sometimes only be conducted on young plants, especially in the case of long-lived perennials.

The objective of this paper is to review published work on the responses of fine roots to changing soil temperatures, so as to provide a synthesis of our

current understanding on belowground responses to a warming planet, and target important hypotheses for future study. We examine the relationships between soil temperature, root growth, root mortality, root respiration and photosynthesis to illustrate what is known about responses of small-diameter tree roots to temperature. The way in which soil temperature interacts with other environmental factors to influence root functioning is emphasized in an attempt to avoid simple generalizations that often confound our understanding of how temperature influences belowground processes. We also bring together published data with a simulation of the exhaustion of nonstructural carbohydrates as a way of bounding the potential influence of temperature on root life span in the absence of acclimation of respiration to changing soil temperatures. Our focus is on fine roots and not their associated mycorrhizas. Clearly, roots and mycorrhizas are intimately related in terms of both form and function (Allen, 1992). Nevertheless, a discussion of mycorrhizal responses to changing soil temperature regimes is beyond the scope of this paper (but see Fitter *et al.*, 2000). We also do not discuss the temperature responses of large, long-lived, structural and/or storage roots.

SOIL TEMPERATURE IN NATURAL ENVIRONMENTS

In temperate, boreal, alpine and arctic soils, average temperatures at a given depth generally increase from spring to mid-summer and then begin to decline. This seasonal pattern has been widely reported and varies with latitude, elevation, topographic position, soil properties, soil drainage, and vegetation type. Soils also warm to progressive depths as the growing season ensues (Kasper & Bland, 1992), again depending on soil properties and vegetation. At high latitudes, soils can be either too cold or permanently frozen close to the surface, inhibiting root activity at certain soil depths throughout the year.

One important and often overlooked aspect of soil temperature is short-term variability. Near the surface, soil temperature can fluctuate widely, again depending on the location and characteristics of the vegetation and soil (Fig. 1). We have found that soil temperatures beneath individual juniper trees in New Mexico can fluctuate by $>10^{\circ}\text{C}$ on hourly time scales 1 cm beneath the soil surface; even at a depth of 5 cm, temperatures are highly dynamic (Fig. 1). The inter-spaces between plants in this open pinyon-juniper woodland exhibit even more remarkable short-term fluctuations in soil temperature to the point that we suspect that the surface 5 cm of soil in the inter-spaces are inhospitable for root growth. Even under a very dense canopy in a mesic northern Michigan sugar maple forest, soil temperatures near the surface, where most fine roots

occur (Hendrick & Pregitzer, 1996), can be quite dynamic (Fig. 1). Temperature fluctuations are greatly dampened with depth, and hourly and daily average temperatures are similar at 10–20 cm in the soil in Michigan, but less so in New Mexico. In many plant communities, a large proportion of fine roots occurs near the soil surface, where variability in soil temperature can be high over relatively short periods of time.

Nutrient availability typically increases with increasing soil temperature because the mineralization of organically bound nutrients is directly related to the temperature-dependent metabolic activity of soil microbes (Shaver *et al.*, 1992; Chapin *et al.*, 1995; MacDonald *et al.*, 1995; Piatek & Allen, 1999; Zak *et al.*, 1999). By contrast, it is very common for the highest levels of soil moisture stress to be associated with high soil temperatures (Teskey & Hinkley, 1981; Piatek & Allen, 1999). Midsummer droughts often come at a time when soil temperatures are at or near their seasonal peak. Responses of roots to changes in soil temperature obviously have the potential to be confounded by root responses to concomitant changes in soil nutrient and water availability. Clearly, field environments can be very different from the simple experimental conditions that are sometimes used to make predictions about root responses to soil temperature.

ROOT GROWTH

Considerable evidence suggests that the rate of extension in root length is positively related to soil temperature, all other factors being equal. Roots grow faster at higher temperatures in annual crop plants (Kasper & Bland, 1992) and perennials (Larson, 1970; Wilcox & Ganmore-Neumann, 1975; Teskey & Hinkley, 1981; Bevington & Castle, 1985; Kuhns *et al.*, 1985; Lieffers & Rothwell, 1986; McMichael & Burke, 1998; King *et al.*, 1999; Weltzin *et al.*, 2000). Many of these observations have come from controlled growth-chamber and glasshouse studies, but field experiments and observational studies report similar results. Agronomists have modeled root growth with depth by using the rate at which soils warm progressively with depth throughout the spring and summer (Kasper & Bland, 1992).

Controlled experiments also demonstrate optimal temperatures for root length extension, with growth rates accelerating up to an optimum temperature and then declining at supraoptimal temperatures (Barney, 1951; Merritt, 1968; McMichael & Burke, 1998). Optimal temperatures for root growth seem to vary widely between different taxa, apparently depending partly on the inherent native temperature regime (Larson, 1970; Tryon & Chapin, 1983; McMichael & Burke, 1998). Nutrient uptake per unit root length also increases with increasing

temperature if plant growth is not limited by other factors (BassiriRad *et al.*, 1993; BassiriRad, 2000). These results are certainly not surprising, given what we know about the relationship between temperature, photosynthesis and shoot growth (Beyschlag *et al.*, 1993; Schwartz *et al.*, 1997). However, as Fitter *et al.* (1998) recently discussed, there is sometimes little correlation between field temperatures and root growth. This is almost certainly related to inherent annual (phenological) patterns of growth and development, and limitations imposed on the plant by other growth-limiting resources above and below ground.

Changes in both moisture and nutrient availability can also drive changes in root growth. Drought clearly causes a decrease in the rate of root length extension (Rogers, 1939; Merritt, 1968; Kaufmann, 1977; Deans, 1979; Teskey & Hinkley, 1981; Bevington & Castle, 1985; Kuhns *et al.*, 1985; Kramer & Boyer, 1995), and drought lowers conductance and canopy assimilation. When high soil temperatures are associated with conditions of drought, there is no *de facto* reason to expect root growth to increase as soil temperatures rise. An increase in soil N availability can also cause an increase in the rate of root length extension (Pregitzer *et al.*, 1995; King *et al.*, 1999; Pregitzer *et al.*, 2000). Because N mineralization increases as soils warm (MacDonald *et al.*, 1995; Piatek & Allen, 1999), it is important to remember that root growth might be responding to multiple soil factors that covary as soil temperatures increase.

SEASONAL PHENOLOGY

Although observational studies clearly document both new root length extension and root mortality throughout the growing season (Hendrick & Pregitzer, 1992), perennial plants exhibit a strongly seasonal pattern of new root production and root mortality, with a burst of production in spring, and significant mortality in the fall (Kuhns *et al.*, 1985; Hendrick & Pregitzer, 1993a, 1996; Wells & Eissenstat, 2000). This seasonal pattern seems to correspond roughly to leaf duration. In temperate forests, the most significant period of root growth corresponds to canopy development in the spring and the most significant period of root mortality corresponds to canopy senescence in the fall (McClagherty *et al.*, 1982; Kurtz & Kimmins, 1987; Hendrick & Pregitzer, 1992, 1993a, 1996). Root–shoot phenological observations of temperate trees presented by Lyr & Hoffmann (1967) suggest that most of the flush of fine-root growth in the spring might occur after canopy development. However, detailed root–shoot physiological and phenological observations are lacking and we simply do not understand whether root growth in the spring precedes, corresponds to, or postdates shoot and leaf

expansion. In deciduous trees and shrubs, any spring root growth that preceded the development of photosynthetically functional new leaves would have to be fueled by the utilization of stored nonstructural carbohydrates.

The breaking of dormancy and the development of new shoots is directly related to increasing temperature in most temperate and boreal plants (Cannell, 1997; Barnes *et al.*, 1998). Shoot development can be predicted with great accuracy from cumulative heat sum in the spring, and natural populations within a species exhibit genetically controlled patterns of heat sum requirements in order for shoots to develop. By contrast, leaf senescence in trees seems to be strongly controlled by photoperiod (Morgenstern, 1996). The periodicity of shoot growth and development in relation to temperature and day length is so well established for some species of trees that it is possible to predict how certain provenances will behave even after they have been relocated from their geographic point of origin to another location with a different temperature and photoperiodic regime (Morgenstern, 1996). At present we do not understand whether root growth in the spring and root mortality in the fall are related to the same environmental cues that drive shoot development and senescence. In temperate deciduous trees with highly determinant patterns of shoot development, such as sugar maple, fine-root growth and mortality seem to be much more continuous and plastic than shoot growth and leaf senescence (Hendrick & Pregitzer, 1992, 1993a, 1996).

The strong flush of root growth in the spring means that considerable root production occurs when soils are still relatively cool. For example, Hendrick & Pregitzer (1996) reported that almost 25% of sugar maple's annual root growth occurred before Julian date 140 (20 May), a period when soils are still cool. Fitter *et al.* (1998), studying an elevation gradient, reported that the initiation of root growth in the spring was progressively later at higher elevations. Presumably, root growth is initiated later at high elevations because the soil warms at a later date. It seems entirely possible that the initiation of root growth in the spring might be related to cumulative heat sum in the soil and that root growth is synchronized with, but lags behind, shoot growth (Lyr & Hoffmann, 1967). This hypothesis needs to be tested. If soil temperatures at a given location warm owing to human-induced climate change, root growth will probably begin earlier in the year. The International Tundra Experiment (Arft *et al.*, 1999) and other high-elevation and high-latitude research (Chapin & Shaver, 1996; Price & Waser, 1998) clearly demonstrate that shoot growth begins earlier in the Northern Hemisphere as air temperatures increase, but comparable experimental root studies have never been conducted. A very interesting

question is whether or not all the meristems in a perennial plant (i.e. shoots and roots) respond to increasing spring temperatures in the same genetically controlled way. If this were true, then root growth would lag behind shoot growth in all perennial plants because soils warm later than the atmosphere in the spring.

ROOT MORTALITY

Most of the extant root length in any perennial plant is dominated by short lateral roots (Weaver, 1958; Pregitzer *et al.*, 1997, 2000). Presumably, main root axes persist for much longer than lateral roots, which grow and die in response to changing soil environmental conditions (Pregitzer *et al.*, 1997). Little is known about the relationship between the form of the absorbing root system and its function. Wells & Eissenstat (2000) have recently demonstrated that larger-diameter 'fine roots' have longer life expectancies than smaller-diameter 'fine roots,' raising the possibility that root longevity is related to position on the branching root system. We do not know how soil temperatures might impact the interactions between root branching and root longevity.

How does increasing soil temperature influence the rate of production and mortality of individual fine roots? Hendrick & Pregitzer (1993b) observed that fine-root longevity was shorter on sites where soil temperatures were higher, but until recently the role of temperature in regulating root life span has received very little experimental attention. Forbes *et al.* (1997), studying ryegrass (*Lolium perenne* var. Parcour) roots, maintained plants in pots at 14, 21 and 27°C. They found that plants at the highest temperatures maintained less root length, and that individual roots had shorter life spans. King *et al.* (1999) found that seasonally elevated soil temperature increased both the production and the mortality of fine-root length in trembling aspen (*Populus tremuloides*), with greater proportional increases in production resulting in greater net root length production (production-mortality).

Although the experimental evidence is very limited, the response so far has been consistent. Rates of fine-root length extension and fine-root mortality increase when soils warm. These results suggest that, if other factors are equal, the growth of new roots and the death of existing roots are accelerated as soils warm. Such a conclusion must be tempered by a deeper understanding of how soil temperature influences seasonal root growth phenology, rates of root respiration, whole-plant source-sink relationships, and the realization that there have not been many experiments designed to understand the interactions between soil temperature, soil moisture, soil nutrient availability, and root growth and mortality.

Extremely low soil temperatures also have the potential to kill fine roots. In Alaska, considerable fine-root mortality might be associated with very low soil temperatures (R. Ruess, pers. comm.). Perennial plants might have to rebuild absorbing root length lost to freezing, a C cost that could vary considerably from year to year depending on snow cover and climate variability. The interactions between low soil temperatures and root growth have not been extensively studied in natural ecosystems (but see Tryon & Chapin, 1983), and there are potentially important questions to resolve. For example, if global warming causes boreal and arctic soils to have higher minimum temperatures, warm faster in the spring, or warm to a greater depth, then patterns of root growth and mortality, and C allocation to root systems, can be expected to change. Simple conceptual or empirical models of the relationships between changing soil temperatures and root growth and mortality are probably inadequate to predict root responses in the future.

ROOT MORPHOLOGY AND TISSUE QUALITY

Soil temperature also has the potential to alter the morphology and tissue quality of the absorbing roots. Kasper & Bland (1992) have reported a positive relationship between accumulated meristem temperature and the number of lateral roots in crop monocots. By contrast, Wilcox & Ganmore-Neumann (1975) have reported that high soil temperatures (27°C) result in fewer lateral branches in red pine (*Pinus resinosa*) than lower soil temperatures (16 and 21°C). In general, there are few investigations of the influence of soil temperature on root morphology. If soil temperature alters nutrient availability or rates of diffusion of nutrients to roots, a change in root morphology might ensue. Little research has focused on how soil temperature alters root tissue quality (King *et al.*, 1996), but root tissue quality might have a key role in regulating how microbial communities respond to a changing global environment (Zak *et al.*, 2000).

ROOT RESPIRATION

Higher temperatures generally result in increased rates of root respiration, and the relationship between rates of respiration and temperature has been widely reported to be exponential. It is often assumed that Q_{10} values are 2.0, that is, respiration rates double for every 10°C increase in temperature. However, there is actually a rather wide range in reported Q_{10} values for roots of tree species, with most values ranging from 2 to 3 (2.7 (Cox, 1975), 1.9–2.1 (Cropper & Gholz, 1991), 1.5–3.0 (Lawrence & Oechel, 1983), 2.0 (Sowell & Spomer, 1986), 2.7 (Burton *et al.*, 1996), 2.1 (Zogg *et al.*, 1996), 2.0 (Ryan *et al.*, 1996), and 2.0 (Bouma *et al.*, 1997)).

Some of this variation might result from the use of different experimental designs by different investigators. It is known that Q_{10} can vary depending on the range of temperatures over which it is determined (Lawrence & Oechel, 1983; Ryan, 1991), with higher values of Q_{10} occurring when low (cold) temperature ranges are examined.

One of the most significant questions yet to be resolved is whether rates of root respiration acclimate to soil temperature. Our laboratory studies of sugar maple suggest that fine roots of this species respond in a generally similar way to increases in temperature throughout the growing season, and little temperature acclimation occurs (Burton *et al.*, 1996, 1998; Zogg *et al.*, 1996). For white spruce, Weger & Guy (1991) also found no evidence that root respiration acclimated to temperature. Similarly, no evidence of temperature acclimation has been found for root respiration in Engelmann spruce (*Picea engelmannii*) or subalpine fir (*Abies lasiocarpa*; Sowell & Spomer, 1986). However, Bryla *et al.* (1997) found that, in citrus seedlings, root respiration acclimated to temperature within 4 d after the temperature of the root system was changed to a different constant temperature. Körner & Larcher (1988) and Fitter *et al.* (1998) have also reported evidence for the acclimation of root respiration to temperature. It could be that species differ in their ability to acclimate to temperature. It is also possible that near-constant temperatures are needed to cause acclimation, and that the natural diurnal and seasonal soil-temperature fluctuations that occur in temperate and boreal ecosystems might prevent acclimation to any large degree in the field. As Fig. 1 demonstrates, field temperatures can fluctuate significantly on hourly and daily time scales, especially near the soil surface, where roots are concentrated in many ecosystems. Step experiments in which temperatures are controlled at different constant set points do not accurately mimic field conditions in many instances. The issue of root respiration acclimating to different temperatures certainly deserves more attention until the contradictory evidence is resolved and the mechanisms controlling root acclimation are understood (Atkin *et al.*, 2000).

It is worth noting that limited evidence clearly supports the notion that root respiration slows (acclimates) during drought (Bryla *et al.*, 1997; Burton *et al.*, 1998). Because field soils are often warm and dry at the same time, the effects of soil temperature and drought on rates of root respiration could easily be confounded. It is also clear that rates of root respiration are directly related to tissue N content (Ryan, 1991; Ryan *et al.*, 1996; Pregitzer *et al.*, 1998). Because the respiration of plant roots is directly related to N concentration, it is possible that increases in root respiration at high temperatures might be due in part to higher rates of N mineralization, which would be promoted when the

soil is warm and moist. All three factors (soil temperature, water and N availability) have the potential to change together in the field and all can directly influence rates of root respiration. We need carefully designed field experiments to clarify the influences of moisture availability, N availability and soil temperature on rates of root respiration.

SIMULATION OF UTILIZATION OF NONSTRUCTURAL CARBOHYDRATES BY USING FIELD TEMPERATURE, MOISTURE AND ROOT NITROGEN CONCENTRATIONS

How long could the fine roots of sugar maple respire without any new nonstructural carbohydrates (TNC)? Using actual field measurements of soil temperature, soil matric potential and root tissue N concentrations, we conducted a simple simulation exercise to explore this question. We assumed no acclimation to temperature; our studies of sugar maple up to this point suggest that little acclimation to temperature occurs (Burton *et al.*, 1996, 1998; Zogg *et al.*, 1996). However, we have reported evidence for reduced rates of fine-root respiration in sugar maple during drought (Burton *et al.*, 1998). The purpose of the simulation was to establish boundary conditions for root life span based on TNC concentrations, and field temperature, moisture and root tissue N conditions. By focusing on the exhaustion of TNC at ambient field conditions during different times of the year, the potential importance of acclimation and/or import of new TNC to roots would, it was hoped, become more apparent. Our detailed field and laboratory studies of fine-root respiration in sugar maple across a range of field temperatures, combined with a program of continuous soil temperature and matric potential monitoring, provided the necessary set of measurements for conducting the simulation.

We surveyed the literature to determine the range in concentration of TNC in the fine roots of trees. In general, the fine roots of trees are 4–6% TNC, ranging to as high as 20% TNC (Table 1). Using actual field temperatures and an empirical relationship that predicts fine-root respiration from soil temperature, soil matric potential and root tissue N concentration, we simulated the exhaustion of TNC reserves at 1% TNC increments from 1% to 15% TNC, which includes most of the range of TNC concentrations reported in Table 1. The approximate time to exhaustion of C supply assumed that there was no temperature acclimation over the duration of the simulation, that no new nonstructural carbohydrate was translocated into the fine roots, that 100% of the TNC in roots was available to support maintenance respiration of existing individual roots, and that TNC (sugar plus starch) is approx. 40% C. This simple hypothetical exercise was designed to enable us to begin to understand how long it was

Table 1. Percentages of total nonstructural carbohydrates (TNC) in fine roots from various sources in the USA

TNC (starches + sugars) (%)	Root diameter (mm)	Species	Location†	Reference
~8–14*	<1	<i>Pinus taeda</i>	NC, OK, AK (fall–winter)	Hallgren <i>et al.</i> (1991)
4–6 soluble sugars	≤1	<i>Populus tremuloides</i>	Northern WI (fall)	J. S. King, pers. comm.
8–12 TNC		<i>Betula papyria</i>		
1.6–8.5	≤0.05	<i>Populus</i> spp.	Clones grown in MI (fall)	Nguyen <i>et al.</i> (1990)
8.5–15	0.05–1	<i>Populus</i> spp.	Clones grown in MI (fall)	Nguyen <i>et al.</i> (1990)
~2.5–0.4‡	≤2	<i>Acer saccharum</i>	VT (spring and fall)	Liu & Tyree (1997)
2–20 (most <10)	Variable	<i>Picea sitchensis</i>	Scotland (May–Aug)	Ford & Deans (1977)
~3.5–6§	<2	<i>Citrus sinensis</i>	FL (fall, winter and spring)	Eissenstat & Duncan (1992)

*Estimated visually from Fig. 1.

†US state names are given as the two-letter abbreviations.

‡Estimated visually from healthy stand values in Fig. 1.

§Estimated visually from unpruned Fig. 1.

Locations of samples and timing of sampling (in parentheses) from each study are included.

Table 2. Average weekly soil temperature and estimated time (wk) before the nonstructural carbohydrate (TNC) content of sugar maple fine roots is exhausted if the only carbon for maintenance respiration is existing TNC

Average weekly soil temperature (°C) TNC (%)	Site A 46° 52' N, 88° 53' W		Site B 45° 33' N, 84° 51' W		Site C 44° 23' N, 85° 50' W		Site D 43° 40' N, 86° 09' W	
	Week 18 8.6°C	Week 32 17.0°C	Week 18 8.7°C	Week 32 17.3°C	Week 18 10.0°C	Week 32 18.3°C	Week 18 11.1°C	Week 32 18.8°C
1	<1	<1	<1	<1	<1	<1	<1	<1
2	<1	<1	<1	<1	<1	<1	<1	<1
3	<1	<1	<1	<1	<1	<1	<1	<1
4	<1	<1	<1	<1	<1	<1	<1	<1
5	1	<1	1–1.5	<1	1	<1	<1	<1
6	1–1.5	<1	1.5–2	1–1.5	1–1.5	<1	1–1.5	<1
7	1–1.5	<1	1.5–2	1–1.5	1–1.5	<1	1–1.5	<1
8	1.5–2	<1	1.5–2	1.5–2	1.5–2	<1	1.5–2	<1
9	2	1–1.5	1.5–2	1.5–2	1.5–2	<1	1.5–2	<1
10	2–2.5	1–1.5	2	1.5–2	1.5–2	1–1.5	1.5–2	<1
11	2.5–3	1.5–2	2–2.5	2	2	1–1.5	1.5–2	<1
12	2.5–3	1.5–2	2–2.5	2–2.5	2–2.5	1–1.5	2–2.5	1
13	2.5–3	1.5–2	2–2.5	2–2.5	2–2.5	1–1.5	2–2.5	1–1.5
14	3–3.5	1.5–2	2.5	2.5	2.5–3	1–1.5	2–2.5	1–1.5
15	3–3.5	2–2.5	2.5–3	2.5–3	2.5–3	1.5–2	2–2.5	1–1.5

Rates of respiration ($\text{g C g}^{-1} \text{ wt wk}^{-1}$) were estimated at the beginnings of week 18 (1 May 1998) and week 32 (7 Aug 1998) and used to calculate the length of time that it would take to exhaust TNC reserves (see the text for details and assumptions).

possible for fine roots potentially to survive without the import of new C from the canopy or reserve C stored elsewhere in the tree.

The root respiration simulation used daily mean soil temperatures (depth 15 cm) and daily mean soil moisture levels (depth 15 cm), which were recorded in four northern hardwood stands during 1998 (Brown *et al.*, 2000). The four stands extend along a 500-km latitudinal gradient from northern to southern Michigan (see Burton *et al.* (1996) for a map of site locations and stand attributes). Yearly precipitation is fairly consistent among the sites; however, the mean annual air temperature decreases from the southern to the northern sites (Burton *et al.*, 1996).

The following empirical relationship from Burton *et al.* (1998) was used to estimate root respiration rates:

$$R_{\text{CO}_2} = (0.058N + 0.622M)e^{0.098T} \quad \text{Eqn 1}$$

(R_{CO_2} , the respiration in $\text{nmol CO}_2 \text{ g}^{-1}$ fine-root biomass s^{-1} ; N , the root N concentration in g kg^{-1} ; M , soil matric potential in Mpa; T , the soil temperature at 15 cm.) The relationship presented in Eqn 1 accurately represented root respiration across all four sites, and there was no apparent evidence of temperature acclimation (Burton *et al.*, 1996, 1998).

Eqn 1 was used to estimate weekly fine-root respiration ($\text{g C g}^{-1} \text{ root wk}^{-1}$) for sites A–D for the weeks of 1 May and 7 August 1998. The average root

N concentration used in the calculations was based on the measurement of roots previously collected at each study site (site A, 17.4 g N kg⁻¹; site B, 18.8 g N kg⁻¹; site C, 18.6 g N kg⁻¹; site D, 17.4 g N kg⁻¹ (Burton *et al.*, 1996)).

The results from the simulation exercise are quite revealing. Given our assumptions, fine roots of sugar maple can live only a matter of weeks in August without new C, regardless of their TNC concentration (Table 2). Typical TNC concentrations of 4–6% result in the consumption of all the TNC in fine roots in <1.5 wk in August at ambient soil temperature and soil matric potential (Table 2). Even during May, when soil temperatures are still relatively cool, we estimated that 4–6% TNC would be gone in <2 wk (Table 2). These results clearly demonstrate two important points. First, understanding acclimation and how the process works is critical, because without acclimation to temperature, root life spans must depend on the continual import of new TNC, even in the short term. Second, it seems very likely that during the growing season, when there are many actively growing root and shoot meristems, rates of fine-root respiration and root longevity might be closely linked to rates of photosynthesis and whole-plant source–sink relationships. As we discuss later, there is already limited evidence for this second conclusion.

WHOLE-PLANT SOURCE–SINK RELATIONSHIPS

How interdependent are the roots and shoots of perennial plants? This question is relevant to understanding the responses of roots to changes in temperature and our simulation suggests that root and shoot activity might be very tightly coupled during the growing season. It seems clear that in some herbaceous plants, photosynthesis and root respiration are directly coupled on time scales that range from minutes to hours (Hansen, 1977; Massimino *et al.*, 1981; Ryle *et al.*, 1985; Amthor, 1994). After reviewing work with annual plants and conducting experiments with single-rooted soybean leaves, Farrar & Jones (2000) argue that C allocation to roots is controlled jointly by roots and shoots. However, the relationships between photosynthesis, C allocation to roots, and rates of root respiration are not well understood in trees and shrubs, which are much larger and longer-lived than annual plants. The average velocity of sugar transport in tree phloem tissue is only a few cm h⁻¹ (Kozlowski & Keller, 1966), and trees and shrubs sometimes have large TNC reserves (Waring & Schlesinger, 1985), so it seems unwise simply to assume that the mechanisms controlling C allocation to roots are the same in annuals and perennials. Nevertheless, some data from trees also suggest a strong and dynamic linkage between rates of canopy assimilation and root respiration.

In a study of whole-tree C allocation with special emphasis on the quantification of C allocation to roots and root respiration, Horwath *et al.* (1994) labeled a block of 3.0-m-tall hybrid poplars (*Populus euramericana* cv. Eugenei) with ¹⁴C₂ in July and in September. They found that the ¹⁴C specific radioactivity of soil respiration peaked 2 d after the addition of ¹⁴C₂ in both July and September. During July, actively growing shoots are a much stronger sink for photosynthate than in September, when, after budset, most of the C assimilated by these genotypes is translocated to the root system (Dickson & Nelson, 1982; Pregitzer *et al.*, 1990). In both July and September, most ¹⁴C had respired from the soil within 100 h of canopy labeling, strongly indicating that root respiration is tightly coupled with canopy assimilation, regardless of whole-tree source–sink relationships. If this is true in most field situations, then root respiration and perhaps fine-root longevity should be linked to rates of canopy C assimilation. However, several key questions remain unresolved.

- How tightly coupled are canopy assimilation and root respiration at different times of the year and during periods of stress that alter root and shoot function?
- How long does it take for the root system to begin to utilize stored nonstructural carbohydrates when environmental stress results in little or no photosynthesis, and how long can roots survive on stored carbohydrates?
- Is the primary mode of coping with stress the down-regulation of fine-root respiration, or do some taxa shed roots during periods of stress?

The Horwath *et al.* (1994) ¹⁴C labeling experiment with trees, and shading experiments with perennial grasses (Billbrough & Caldwell, 1995), both suggest that fine-root respiration is closely linked to canopy assimilation. We expect that this would be especially true during the growing season, when there are hundreds to thousands of active meristems at the whole-tree level and sink strength is high at many locations within the tree. Fitter *et al.* (1998) recently reported that root respiration along an elevational gradient of grasslands was most closely correlated with preceding radiation, also suggesting that canopy assimilation and root respiration might be tightly linked in grasslands. In general, we hypothesize that rates of root respiration are directly linked to rates of canopy assimilation in perennial plants, probably with time lags that are no longer than a few days. Any environmental factor altering rates of whole-canopy assimilation would eventually also influence root respiration, but the time scales involved are very poorly understood in trees. This hypothesis could potentially explain how variable environmental conditions regulate root respiration. If soil temperatures increase, and water and nutrients are sufficient, the

rates of both canopy assimilation (Schwartz *et al.*, 1997) and root respiration increase (Burton *et al.*, 1998). If soil temperatures are high but drought inhibits conductance and assimilation, rates of root respiration decline. This hypothesis should be reasonably straightforward to test. If the hypothesis is not true, fine-root respiration over significant periods of decreased photosynthesis must depend on stored nonstructural carbohydrates, implying that the root and shoot systems are decoupled in time in their response to changing environmental conditions, an unlikely scenario. The idea that root respiration rapidly adjusts to temperature in all situations seems overly simplistic. Factorial field experiments that create dynamic 'hot-wet' and 'hot-dry' soil conditions that significantly alter rates of conductance and photosynthesis should prove useful in understanding how root respiration responds to temperature as multiple growth-limiting soil conditions change during the growing season (Bilbrough & Caldwell, 1995).

It is important to note that we do not have a clear understanding of how tightly coupled in time canopy assimilation and root functioning are over the range of environmental conditions that perennial plants typically experience in the field. Gebauer & Ehleringer (2000) recently demonstrated that, in dry environments, water and N uptake in shallow roots need not necessarily occur simultaneously. These results indicate that different parts of the root system might be responsible for the acquisition of different essential resources at different times. How widespread this phenomenon might be, and how the acquisition of soil resources is related to root respiration, and to canopy physiology, are new and interesting areas for additional whole-plant research. It seems we have a rather incomplete picture of how the whole plant responds to dynamic changes in temperature, moisture, nutrients and sunlight, even though these essential resources often covary in the field through time. This conclusion seems particularly true for large, deeply rooted perennial plants, which typically have significant quantities of stored energy and strongly seasonal patterns of root and shoot development. We clearly need more field studies of full-size plants that are more than a few months old.

CONCLUSIONS

Rates of root growth and mortality increase with temperature if other factors do not limit photosynthesis and respiration. We hypothesize that in temperate and boreal environments, the initiation and rate of new root growth in the spring are directly related to cumulative heat sum in the soil. Global warming will result in earlier root growth in the spring, and if other factors do not limit C assimilation, soil warming will result in greater root

production and mortality, and greater root C flux to the soil. The influence of soil temperature on root functioning in boreal and tundra environments clearly needs additional study. In these cold regions where the proportional allocation of C to roots and mycorrhizae are high and C storage is great, surface soil temperatures must have a key role in determining when roots grow, how they function and perhaps whether they die. Our simulations of fine-root respiration, and the limited literature, suggest that during the growing season fine roots must depend on the import of new C to survive for even limited periods. We hypothesize that rates of fine-root respiration in summer are tightly coupled with rates of conductance and photosynthesis. However, the way in which soil temperature, soil water, soil nutrients and sunlight interact to control root respiration, root growth and root mortality is very poorly understood in large, perennial plants.

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