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RESEARCH PAPER

Interactive effects of soil temperature and moisture on Concord grape root respiration

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Abstract

Root respiration has important implications for understanding plant growth as well as terrestrial carbon flux with a changing climate. Although soil temperature and soil moisture often interact, rarely have these interactions on root respiration been studied. This report is on the individual and combined effects of soil moisture and temperature on respiratory responses of single branch roots of 1-year-old Concord grape (*Vitis labruscana* Bailey) vines grown in a greenhouse. Under moist soil conditions, root respiration increased exponentially to short-term (1 h) increases in temperature between 10 °C and 33 °C. Negligible increases in root respiration occurred between 33 °C and 38 °C. By contrast to a slowly decreasing Q_{10} from short-term temperature increases, when roots were exposed to constant temperatures for 3 d, the respiratory Q_{10} between 10 °C and 30 °C diminished steeply with an increase in temperature. Above 30 °C, respiration declined with an increase in temperature. Membrane leakage was 89–98% higher and nitrogen concentration was about 18% lower for roots exposed to 35 °C for 3 d than for those exposed to 25 °C and 15 °C. There was a strong interaction of respiration with a combination of elevated temperature and soil drying. At low soil temperatures (10 °C), respiration was little influenced by soil drying, while at moderate to high temperatures (20 °C and 30 °C), respiration exhibited rapid declines with decreases in soil moisture. Roots exposed to drying soil also exhibited increased membrane leakage and reduced N. These findings of acclimation of root respiration are important to modelling respiration under different moisture and temperature regimes.

Key words: Carbohydrates, Concord grape, membrane leakage, root respiration, soil water content, temperature, *Vitis labruscana*.

Introduction

Respiration, as a controlled and multiple-stepped combustion of carbohydrates, provides energy for various cellular activities, as well as carbon skeletons for biosyntheses of functional and structural substances. In roots, respiratory energy is used for nutrient uptake, and root growth and maintenance, as well as for symbiotic processes and defence (Martinez *et al*., 2002). Root respiration accounts for 33–60% of total soil respiration (Bowden *et al*., 1993; Pregitzer *et al*., 1998), and consumes 8–52% of carbon fixed by photosynthesis (Lambers *et al*., 1996). Roots exert a strong influence on the temperature sensitivity of soil CO_2 efflux (Boone *et al*., 1998) and provide an important reference for global warming caused by an increase in atmospheric CO_2 concentration (Atkin *et al*., 2000).

Root respiration is subjected to the influences of environmental factors, including temperature, moisture, and nutrients (especially nitrogen) (Zogg *et al*., 1996; Atkin *et al*., 2000; Maier and Kress, 2000; Bryla *et al*., 2001). Under cold soil conditions (i.e. <10 °C), root respiration is low and roots accumulate reducing sugar and nitrogen while consuming starch (Lunackova *et al*., 2000; Covey-Crump *et al*., 2002). With an increase in temperature, respiration increases and is generally modelled as increasing exponentially with temperature, with a Q_{10} (the proportional increase in respiration for every 10 °C rise in temperature) near 2.0 (Cox *et al*., 2000). However, this is true only over

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a limited temperature range, as more often Q_{10} itself is temperature dependent, decreasing with an increase in measurement temperature (Atkin *et al*., 2000; Desrochers *et al*., 2002; Atkin and Tjoelker, 2003).

Sensitivity of respiration to temperature (Q_{10}) differs among root ages and/or orders (Palta and Nobel, 1989; Desrochers *et al.*, 2002) and species (Atkin *et al*., 2000; Pregitzer *et al*., 2000; Covey-Crump *et al*., 2002; Loveys *et al.*, 2003). Respiration of young roots (lower order or finer roots) is much higher and much more sensitive to temperature than old (coarse) roots (Palta and Nobel, 1989; Desrochers *et al.*, 2002). Arctic and temperate species often exhibit greater increases in Q_{10} with an increase in measurement temperature compared with tropical species (Atkin and Tjoelker, 2003).

The widely observed acclimation of root respiration to temperature changes (Tjoelker *et al.*, 1999; Atkin *et al*., 2000; Bryla *et al*., 2001; Atkin and Tjoelker, 2003; Loveys *et al*., 2003) necessitates the distinction between short-term and long-term temperature effects, which complicates modelling of respiratory responses to temperature. Acclimation of root respiration is defined as the subsequent adjustment in respiration rate to compensate for the initial change in temperature (Atkin *et al*., 2000). It can occur in only a couple of days following shifts in temperature (Bryla *et al*., 2001; Covey-Crump *et al.*, 2002). Cold-acclimated roots tend to respire faster under warm measurement temperatures than warm-acclimated ones (Atkin *et al.*, 2000; Atkin and Tjoelker, 2003). Acclimation of root respiration to high temperatures results in a reduction in Q_{10}. Changes in ATP demand, respiration pathways, and substrate availability, as well as in respiratory enzyme capacity, may be involved in temperature acclimation (Atkin and Tjoelker, 2003). The degree of acclimation of respiration to changes in temperature differs among species (Atkin *et al*., 2000; Pregitzer *et al.*, 2000; Covey-Crump *et al.*, 2002; Atkin and Tjoelker, 2003), varying from little acclimation in sugar maple (Burton *et al.*, 1996; Burton and Pregitzer, 2003), red pine (Burton and Pregitzer, 2003), white spruce (Weger and Guy, 1991), and Engelmann spruce (Sowell and Spomer, 1986), to complete acclimation (homeostasis) in citrus (Bryla *et al*., 1997).

Fluctuations in soil temperature and soil moisture are closely linked, but rarely studied together (but see Bryla *et al*., 2001). Soil moisture not only directly affects root physiology, but also indirectly by affecting soil thermal properties. Thus, dry soils typically fluctuate much more widely in daily temperature than wet soils. At moderate temperatures, soil moisture exerts a substantial influence on root respiration. Root respiration decreases as soil moisture is depleted (Palta and Nobel, 1989; Burton *et al*., 1998; Huang and Fu, 2000; Maier and Kress, 2000; Bryla *et al.*, 2001). Citrus roots maintain viability (Eissenstat *et al.*, 1999) and exhibit basal root respiration when exposed to dry soil (Bryla *et al*., 2001). The influence of soil moisture is also temperature dependent. Under moderate to high temperature conditions (20–35 °C), drought-induced reductions in root respiration in citrus were much more drastic than at a lower temperature (15 °C) (Bryla *et al*., 2001).

In previous work on citrus (Bryla *et al*., 2001), strong interactions of soil moisture with temperature on root respiration were found that have important implications on how respiration should be modelled under different climate-change scenarios, where both elevated temperatures and increasing drought occur. Citrus may be unique in its temperature and moisture responses, not only because it is a subtropical evergreen, but also because of its tough, coarse roots with relatively slow respiration rates and long lifespan, even in very dry soils (Bryla *et al.*, 1997; Eissenstat *et al*., 1999, 2000; Bouma *et al*., 2001). Concord grape is more typical of temperate fruit crops in that its finest lateral roots tend to be thin and succulent with high uptake capacity and metabolism in young roots and a fairly short lifespan (grape: Comas *et al*., 2000; Anderson *et al*., 2003; Volder *et al*., 2005; apple: Eissenstat *et al*., 2000; Wells and Eissenstat, 2001; peach: Wells *et al.*, 2002). Like most temperate fruit crops, portions of the root system of Concord grape can be exposed to wide ranges of soil moisture and soil temperature. For example, in Fredonia, New York where Concord root dynamics have been studied over a number of years (Anderson *et al*., 2003; Comas *et al*., 2005), volumetric soil moisture content can vary from <5% to >20% (Anderson *et al*., 2003) and maximum daily soil temperatures at a 5 cm depth frequently reach 35–40 °C in July and August (AN Lakso *et al*., unpublished data). Here is a report on the quantitative effects of soil temperature, soil moisture, and various combinations of the two factors, on respiration, soluble carbohydrates, nitrogen, and electrolyte leakage in Concord grape roots. Unlike citrus, Concord grape was expected to be less tolerant of soil moisture and high temperatures but more tolerant of lower temperatures.

Materials and methods

Plant materials and growing conditions

The experiment was conducted from November 2003 to March 2004 with 16, 1-year-old own-rooted 'Concord' vines grown individually in sandy soil in 36 l pots (50 cm×30 cm×30 cm deep) in a greenhouse. Six of the plants were used for respiration measurements of individual intact root branches. They were irrigated every 3 d until the containers drained freely of water. The remaining 10 plants were used to study the effects of soil moisture deficits on root respiration and membrane leakage. Five pots were fully irrigated with 2.0 l of water each day and five pots were irrigated with only 0.1 l each day. Greenhouse air temperatures ranged between 20 °C and 30 °C, relative humidity ranged between 50% and 70%, and light was supplemented with four 400 W halide lamps from 07.00 h to 19.00 h each day.

Estimating respiration of individual intact root branches

The gas exchange system for estimating respiration of intact roots was designed to have air continuously flow through the chambers

during the entire period of the experiment to allow steady-state conditions to develop between root respiration and gas exchange with the chamber headspace (Fig. 1). The root chamber design was similar to that used by Bryla *et al*. (2001) with some modifications. Chamber lids were each installed with two ports sealed with rubber septa, through which water could be injected into the chamber as a means of irrigation. Temperature inside the chambers was controlled by water circulating through the U-shaped stainless-steel tube inside the chambers from a water bath. All the chambers were wrapped with black insulating foam to minimize heat transfer between the chamber soil and the soil at ambient temperatures outside the chamber.

An attached root branch was uncovered from each vine (pot) and placed inside the chambers, maintaining the root in its same growth orientation (Fig. 2). Each chamber was filled with 50 ml of sterilized sandy soil wetted with 15 ml of deionized water. A 0.25-mm-diameter copper-constantan thermocouple was then placed close to the root at the centre of the sandy soil to monitor the chamber temperature. When respiration measurements were not being conducted, humidified ambient air was pumped into each chamber at a flow rate of 360 ml min^{-1} (Fig. 1A). During measurement, the three-way valve was switched to a tube connected to the Li-Cor-6200 gas exchange analyser (Li-Cor Inc., Lincoln, NE; Fig. 1B), maintaining an airflow of

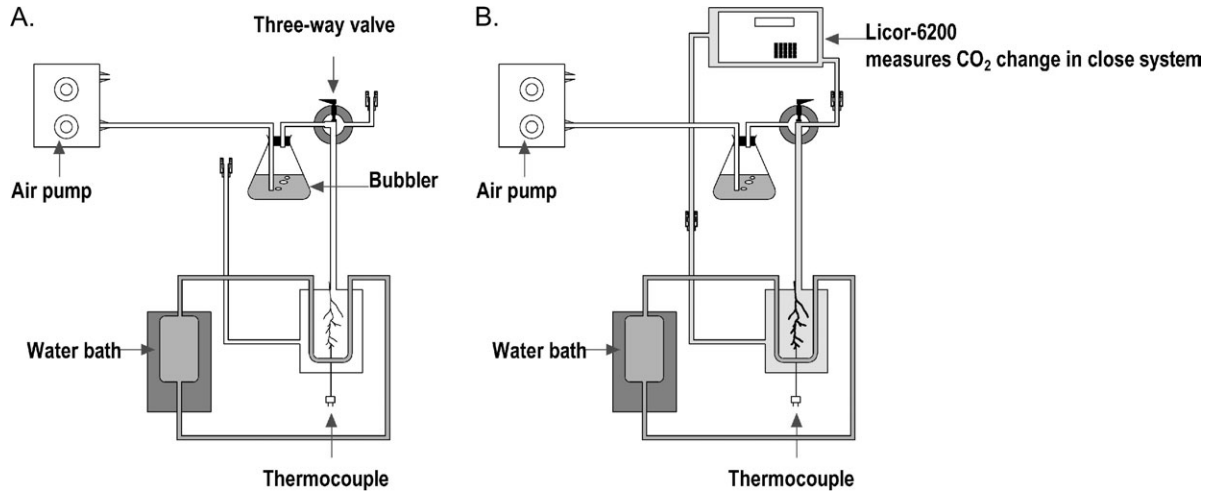


Fig. 1. Schematic drawing of the gas exchange system for intact roots. The construction of the root chambers was based on Bryla *et al*. (2001). Circulating water running through the U-shaped stainless-steel tube inside the root chamber was temperature-controlled by a water bath. The soil temperature inside the chamber was read with a thermocouple reader at the time of respiration measurement. (A) System before and after respiration measurement. Air, flowing at a rate around 360 ml min^{-1}, was pumped through a water bubbler before entering the chamber. The water bubbler humidified the air to minimize desiccation. (B) The system during respiration measurement. The three-way valve is switched to the outlet tube of a Li-Cor-6200 gas analyser, while the airflow outlet tube of the chamber is connected to the inlet tube of the analyser. A closed circuit of airflow is then pumped by the analyser at a rate around 360 ml min^{-1}. The CO_2 concentration increase inside the root chamber was determined.

Fig. 2. Illustration of Concord grape roots being put in the respiration chamber. The wires are a fine-wire thermocouple.

360 ml min^{-1}. The rate of CO_2 concentration increase inside the closed system was determined using the closed system of the Li-Cor-6200.

Temperature effects on root respiration

To determine the effects of short- and long-term exposure to a particular set temperature, root respiration (expressed as nmol CO_2 g^{-1} root DW s^{-1}) was determined at the following chamber temperatures: (i) 5 °C increments every 1 h between 10 °C and 40 °C; (ii) 5 °C increments every 3 d between 10 °C and 40 °C; (iii) 20 °C, 30 °C, 20 °C, each for 5 d; and (iv) 20 °C, 10 °C, 20 °C, each for 5 d. The number of replicates (chambers) for the above temperature trials was six, five, four, and three, respectively. After a particular set of temperature measurements was finished, roots in the chambers were harvested. The temperature response of soil CO_2 release with no roots served as the blank. Harvested roots were washed with tap water, oven-dried at 65 °C for 3 d and weighed. The temperature response of respiration, Q_{10}, was calculated according to the formula (Atkin and Tjoelker, 2003):

$$Q_{10} = (R_{T_2}/R_{T_1})^{10/(T_2-T_1)} \quad (1)$$

where R_{T_2} and R_{T_1} represent respiration at temperature (°C) T_2 and T_1, respectively.

Interaction of temperature and soil moisture on intact root respiration

Soil moisture was determined by time domain reflectrometry (TDR; Topp, 1993). TDR probes (unbalanced design) with 10-cm-long stainless-steel rods at a distance of 1.5 cm apart were inserted into the chamber from one end. A Tektronix cable tester interfaced with a computer equipped with specialized software (developed by Ron Hubbard, Department of Plant, Soils and Biometeorology, Utah State University) was used for determination of the soil water content inside the chamber. The TDR estimates were calibrated with soil water content determined gravimetrically. To assess the influence of soil drying on root respiration, water was withheld from the chambers controlled at 10 °C, 20 °C, and 30 °C. In addition, the airflow did not go through the bubbler (see Fig. 1). For chambers controlled at 10 °C, the airflow passed through desiccant (silica gel) added to the flasks previously serving as bubblers (Fig. 1). Roots were exposed to each temperature in wet soil (water content around 30%) for at least 3 d before respiration was estimated. Water content and respiration were measured at 08.00, 12.00, and 16.00 h every day until the soil moisture decreased from about 30% to around 5% (volumetric water content). The roots were then harvested and dried in an oven at 65 °C for 48 h. Root tissue (5 mg DW) from each chamber was analysed for total nitrogen concentration by flash combustion chromatography (Fisons CHNS-O elemental analyser, Model EA-1108).

Other physiological changes in roots at different temperatures

Intact single roots were sealed in the chambers and respectively exposed to 15, 25, and 35 °C. Roots were harvested 1, 3, and 5 d after temperature exposure. The samples were rinsed with deionized water, and immersed in 40 ml deionized water at room temperature. Electrical conductivity (EC) of the water was measured with an EC meter (model Orion-105) 30 min and 60 min after root immersion. Roots were then scanned with a desktop scanner and weighed. Membrane leakage was calculated as the increase of EC within 1 h per unit fresh weight of root (μs cm^{-1} h^{-1} g^{-1} FW). The roots were then dried (65 °C for 48 h). Soluble sugars in the roots were extracted with 80% (v/v) ethanol solution and analysed photometrically by the anthrone method (Zhang, 1990). Nitrogen content in the samples was determined as previously described.

Effects of drought on respiration and membrane leakage

Roots were excised from potted vines experiencing limited irrigation (100 ml d^{-1} in the drought treatment versus 2000 ml d^{-1} in the well-watered control). Respiration at 25 °C was determined on the excised root branches composed of first and second order roots using a Clark-type oxygen electrode (Hansatech Oxygraph, King's Lynn, UK). Other root samples were used to estimate percentage membrane leakage of electrolytes. Electrical conductivity of the water was measured 30 min after root immersion, and then the sample was boiled in the water for 5 min to disrupt the membranes of the root cells completely. After the water was cooled to room temperature and brought to volume, total electrolytes (EC_t) in the roots were estimated. Membrane leakage was calculated as the percentage of EC measured after 30 min relative to EC_t.

Results

Responses of roots to short- and long-term temperature exposure

Respiration rate of Concord grape roots increased with short-term (1 h) increases in temperature from 10 °C to 37.6 °C (Fig. 3A). The relationship fitted an exponential

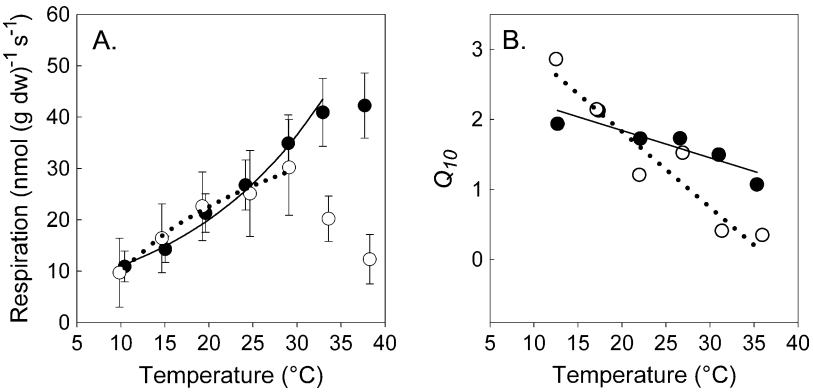


Fig. 3. Respiratory responses of roots in moist soil to changes in temperature. (A) Respiration of roots exposed to each temperature for 1 h (n=6; filled circles and continuous line between 10 °C and 32 °C; y=6.04e$^{0.0599x}$, R^2=0.988) and for 3 d (n=5; open circles and dashed line between 10 °C and 28 °C; y=18.3ln(x)−32.3, R^2=0.987). (B) Respiratory Q_{10} of roots exposed to each temperature for 1 h (continuous line; y=−0.039x+2.63, R^2=0.809) and 3 d (dashed line; y=−0.106x+3.98, R^2=0.899). The temperature shown on the x-axes represents the middle value between each temperature increase.

curve up to 33 °C (y=6.04e$^{0.60x}$, R^2=0.99) reasonably well. The Q_{10} exhibited a linear decrease as temperature increased (y=−0.039x+2.62, R^2=0.81, P=0.038) (Fig. 3B). Respiration of roots maintained at various temperatures for 3 d increased logarithmically [y=18.3ln(x)−32.3, R^2=0.99] from 10 °C to 30 °C and decreased dramatically at 33 °C or above (Fig. 3A). Respiratory Q_{10} decreased linearly with an increase of temperature at a steeper slope (y=−1.06x+4.00, R^2=0.90, P=0.005) compared with short-term temperature exposure (Fig. 3B). Q_{10} dropped to <1.0 when roots were exposed to soil temperatures above 30 °C for 3 d. Many succulent roots maintained at 35 °C for >3 d turned brownish black, an indicator of root death in grape (Comas *et al.*, 2000), and exhibited increased tissue ion leakage as compared with those maintained at 15 °C and 25 °C (Fig. 4). Sugar content in roots exposed to these temperatures for 3 d was not significantly affected by temperature (18.9 ± 2.1 mg g^{-1} DW, 17.6 ± 1.4 mg g^{-1} DW, and 21.1 ± 2.1 mg g^{-1} DW, respectively, for 15 °C, 25 °C, and 35 °C).

The time-course of respiration when a small portion of a plant's roots were exposed to lower or higher temperatures than temperatures of the bulk root system (~20 °C) indicated that acclimation occurs at warm (30 °C) but not at cold (10 °C) temperatures (Fig. 5). Respiration of roots grown at 20 °C increased from 29.9 nmol CO_2 g^{-1} DW s^{-1} to 45.2 nmol CO_2 g^{-1} DW s^{-1} (Q_{10}=1.51) after 1 d of exposure to 30 °C (Fig. 5A). Respiration began to decrease with continued exposure to 30 °C. When soil temperature was reduced from 30 °C to 20 °C, root respiration dropped initially from 26.2 nmol CO_2 g^{-1} DW s^{-1} to 17.5 nmol CO_2 g^{-1} DW s^{-1} (Q_{10}=1.54) and then gradually increased to original levels. When temperature was decreased from 20 °C to 10 °C, respiration dropped from 36.0 to 13.0 nmol CO_2 g^{-1} DW s^{-1} (Q_{10}=2.8) and remained at this rate (Fig. 5B). As temperature was adjusted back to 20 °C, respiration increased to close to the original level.

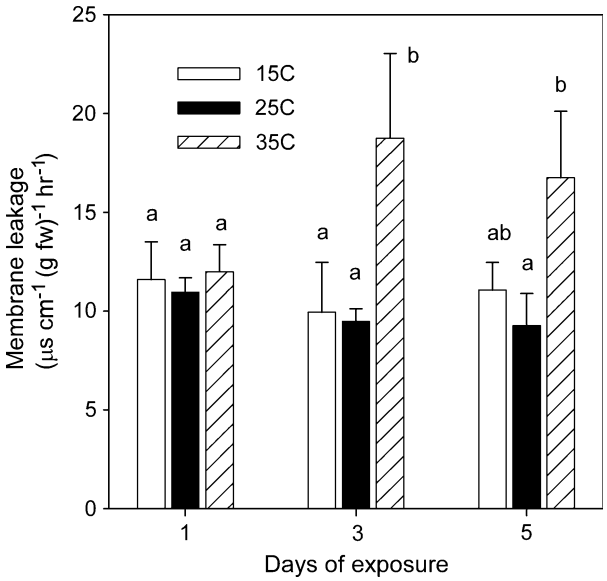


Fig. 4. Membrane leakage in root after exposure to different temperatures for 1 d, 3 d, and 5 d. Roots were sampled from separate chambers at 15 °C, 25 °C, and 35 °C after 1 d, 3 d, and 5 d (n=4–6; different chambers for each harvest date). Different letters above the columns indicate significant difference at P=0.05 based on LSD test and two-way ANOVA.

Response of root respiration to soil moisture

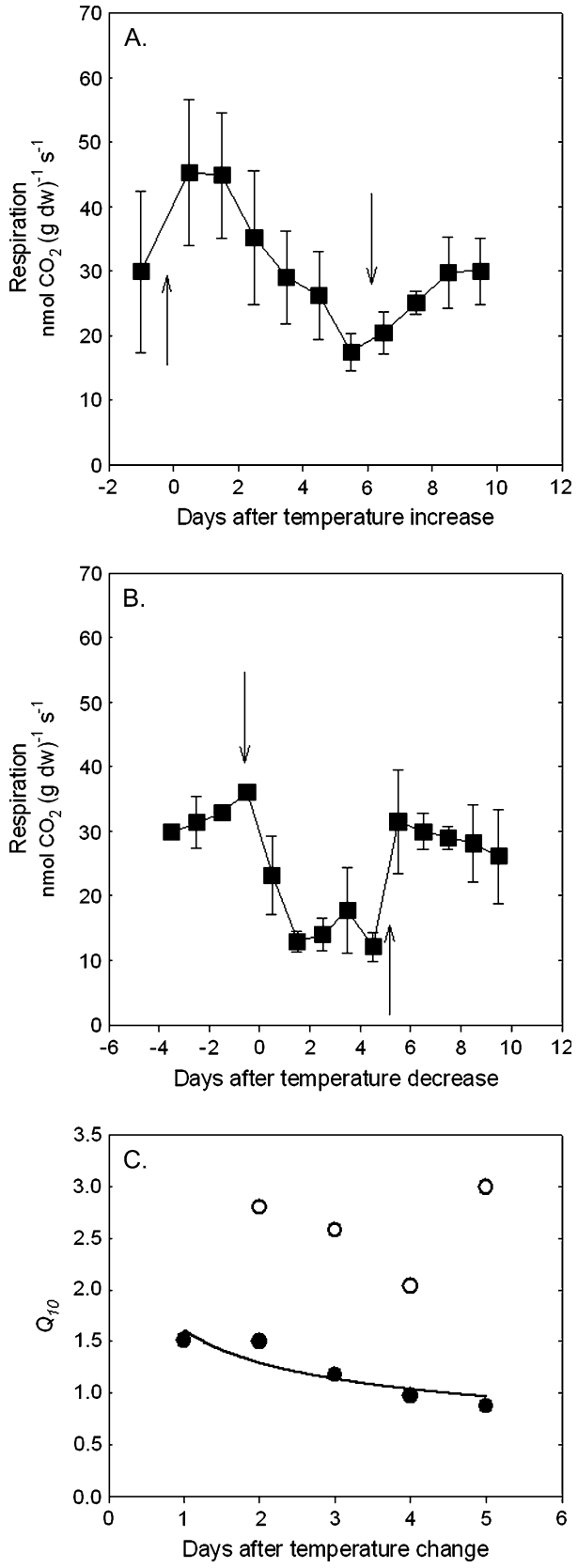
Root respiration decreased logarithmically [y=12.25ln(x)−3.59, R^2=0.66] with the depletion of soil moisture, while membrane leakage of root cells increased (Fig. 6). Respiration was lower in higher-ordered, coarser roots when soil moisture was not limiting (well-watered pots; Fig. 7; correlation coefficient between respiration and root order r=−0.999, P=0.026*). Under drought conditions (water content <5%), root respiration of all different root orders was reduced and displayed an opposite trend from the well-watered roots; an increase in root order corresponded with an increase in respiration. The magnitude of respiratory reduction caused by soil drought was 90%, 73%, and 56%, respectively in first-, second-, and third-order roots (correlation coefficient between respiration and root order r=0.951, P=0.142), suggesting the finer roots of the lower orders may be more sensitive to drought than higher-order roots.

Interaction of temperature and soil moisture in root respiration

At both 20 °C and 30 °C, respiration decreased logarithmically with depletion of soil moisture with essentially no difference between the two temperatures. At 10 °C, however, respiration was closer to a basal level, exhibiting only a small decrease in respiration with a decrease in soil moisture (Fig. 8). Using the regressed curves of respiration against soil moisture at 10 °C [y=4.589 ln(x)−3.470, R^2=0.912], 20 °C [y=11.63ln(x)−12.19, R^2=0.561], and 30 °C [y=13.97ln(x)−17.64, R^2=0.920], the respiratory Q_{10} was calculated at soil water contents of 5%, 10%, and 20%. The Q_{10} tended to be smaller at lower moisture contents. At 5%, 10%, and 20% soil water content, Q_{10} was, respectively, 1.68, 2.07, and 2.22 for 10–20 °C and 0.70, 0.99, and 1.06 for 20–30 °C. Soil moisture deficits also caused a significant decrease of N in the root, yet roots exposed to low temperature (10 °C) tended to retain a higher N content compared with those at higher temperatures (Fig. 9). When soil moisture was sufficient, root N exhibited no difference between 15 °C and 25 °C, but tended to decrease at 35 °C (Fig. 9).

Discussion

A quantitative description of root respiration to changes in soil temperature and moisture is important to plant growth modelling and predicting climate change associated with



increases in atmospheric CO_2. The present results are some of the first quantitative descriptions of root respiration in plants as a function of short- and long-term exposures to temperature and in response to decreases in soil moisture. It has also clearly been demonstrated that there can be important interactions—roots in cold soil are less responsive to changes in soil moisture than comparable roots in warm soil. Lastly, succulent fine roots like those in grape may exhibit losses in membrane integrity when exposed to dry soil or high temperatures.

When soil moisture is not limiting, temperature acts as the dominant environmental factor affecting root respiration (Atkin *et al.*, 2000; Bryla *et al.*, 2001). Response of root respiration to short-term increases in soil temperature is generally expressed exponentially with a Q_{10} around 2.0 in many plants (Salisbury and Ross, 1996). However, the exponential response is true only in a limited range of temperatures (Atkin and Tjoelker, 2003). Bryla *et al.* (2001) showed that, in orange, a typical subtropical fruit crop, root respiration increased exponentially with short-term increases in soil temperature between 10 °C and 40 °C. The present results in Concord grape (Fig. 3A), a species native to the cool climate of the north-east United States, displayed a similar trend, but for a narrower temperature range (below 33 °C). Respiration showed essentially no increase as temperature rose above 33 °C. As observed in leaves, and to a lesser extent, in roots of other species (Atkin *et al.*, 2000; Desrochers *et al.*, 2002; Atkin and Tjoelker, 2003), respiratory Q_{10} in Concord grape roots exhibited a linear decline with a temperature increase from 10 °C to 38.5 °C (Fig. 3B). Atkin and Tjoelker (2003) found that the magnitude of respiratory response to temperature changes varies according to plant origin, with Q_{10} of leaves of tropical species being less reduced with temperature increase than leaves of temperate, boreal, and arctic species. Similar conclusions can be drawn from a comparison of work with roots of subtropical citrus (Bryla *et al.*, 2001) and temperate grape (this study).

Long-term temperature changes elicit a different respiratory response from short-term temperature changes as a result of temperature acclimation (Bryla *et al.*, 2001; Figs 3, 5). Acclimation to a new temperature may take place

Fig. 5. Time-course of root respiration (±standard error) in response to changes in soil temperature. (A) Soil temperature was controlled at 20 °C before day 0, at which time it was adjusted to 30 °C, indicated by the upward-pointing arrow (n=4). After 4 d, the temperature was reduced back to 20 °C, as indicated by downward-pointing arrow and remained at 20 °C for an additional 5 d. (B) Soil temperature was controlled at 20 °C before day 0, at which time it was adjusted to 10 °C, as indicated by the downward-pointing arrow (n=3). After 4 d, temperature was increased back to 20 °C, as indicated by upward-pointing arrow and remained at this temperature for 5 d. (C) Changes of Q_{10} after temperature changes. Open circles (no line), Q_{10} against days after temperature drop from 30 °C to 20 °C (R^2=0.000, P=0.99); filled circles and continuous line, power regression of Q_{10} against days after temperature increase from 20 °C to 30 °C (y=1.66$x^{-0.359}$, R^2=0.846, P=0.027).

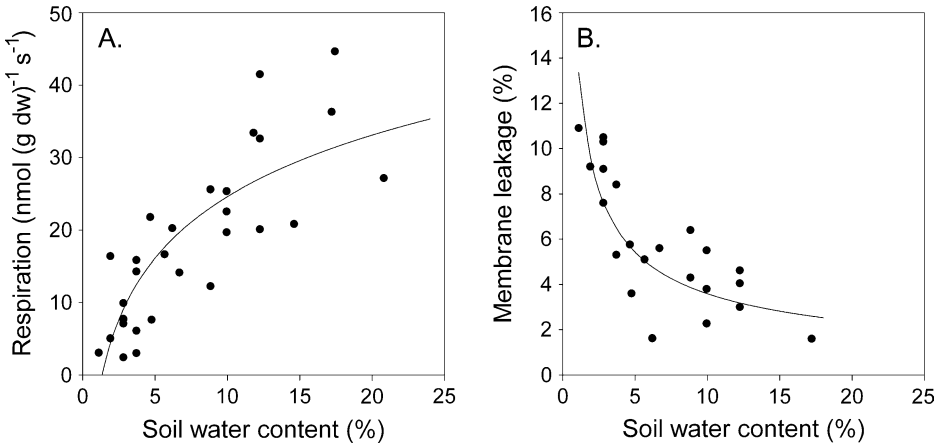


Fig. 6. Effects of soil moisture on root respiration (A) and degree of membrane leakage (B) for roots at 25 °C.

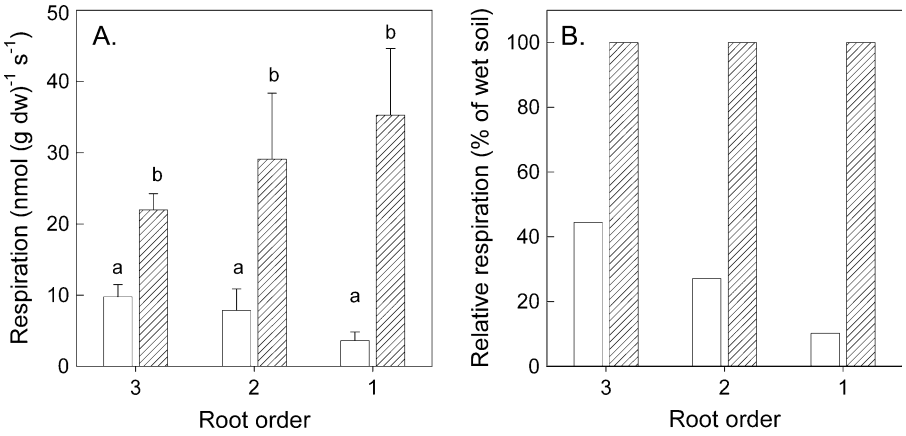


Fig. 7. Respiration of different root orders in dry (open columns, n=4) and wet (hatched columns, n=3) soils: (A) actual respiration and (B) respiration relative to that of roots in wet soil. First-order roots bear no lateral roots, second-order roots bear one level of branching, and so on.

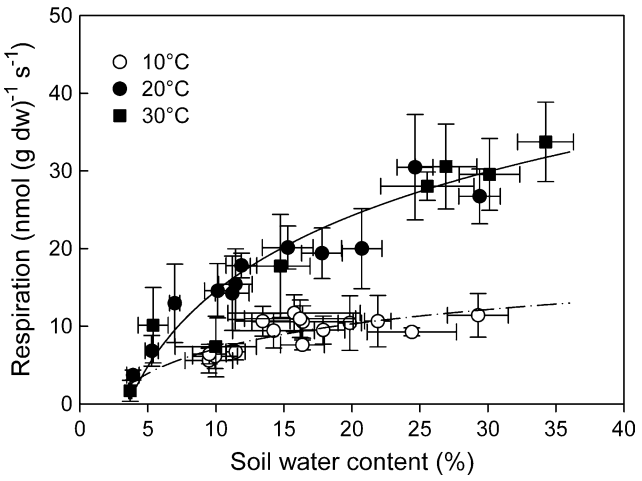


Fig. 8. Response of root respiration to changes in soil moisture at soil temperatures of 10 °C (n=3 for 15 d), 20 °C (n=4 for 12 d) and 30 °C (n=3 for 15 d). Continuous line, logarithmic regression of root respiration response to soil moisture change at 20 °C and 30 °C (y=14.0ln(x)−17.6, R^2=0.920); thick dashed line: logarithmic regression of root respiration response to soil moisture change at 10 °C (y=4.59ln(x)−3.47, R^2=0.561).

within a couple of days (Bryla *et al.*, 2001; Covey-Crump *et al.*, 2002). Like citrus, respiration of Concord grape root acclimates to new temperatures (e.g. from 20 °C to 30 °C), but it may take more than 4 or 5 d for Concord grape root respiration to acclimate and reach a homeostatic level (Fig. 5). The respiration of roots acclimated to a new constant temperature for 3 d displayed a logarithmic change with temperature increase within 30 °C and decreased when temperatures rose above 33 °C (Fig. 3A).

The Q_{10} of acclimated respiration decreased more sharply with temperature increase than non-acclimated respiration (Fig. 3B). Atkin and Tjoelker (2003) attributed Q_{10} reduction at higher temperatures to limitation of substrate and/or adenylate turnover. Some evidence is provided here that the decrease of Q_{10} in Concord grape was not caused by substrate limitation, as the sugar content in roots was not different between lower and higher temperatures. However, a more complete understanding of substrate limitations also requires estimates of starch reserves, which was not determined in this study.

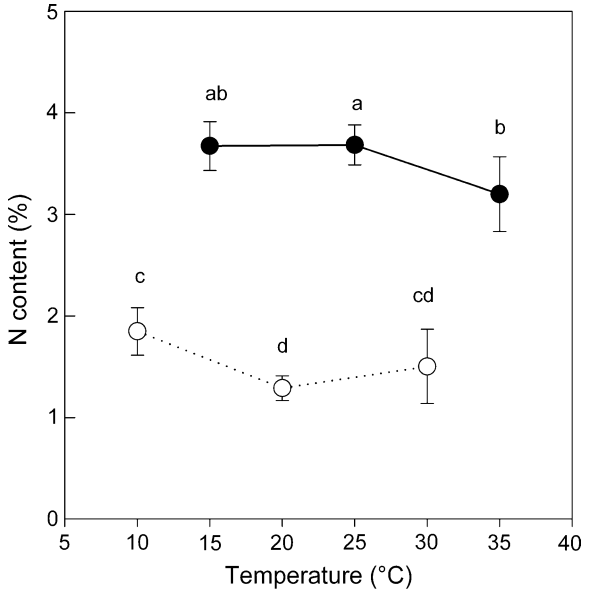


Fig. 9. Effects of soil temperature and moisture on nitrogen concentration in Concord grape roots. Dashed line and open circles, roots experienced soil drying under different temperatures. Samples were analysed when the soil moisture was reduced to around 5%. Continuous line and closed circles, roots exposed to different temperatures in well-watered soil for 3 d. Different letters above each point indicate significant difference at P=0.05 based on LSD test, one-way ANOVA.

Sustained higher soil temperatures shorten the lifespan of ephemeral roots (Pregitzer *et al.*, 2000; Atkinson *et al.*, 2003). The present study suggests that a temperature of 33 °C or higher caused part of the succulent root of Concord grape to die within 3 d, as reflected by a drop in respiration (Fig. 3) and membrane leakage increase (Fig. 4). The increase of tissue ion leakage indicates loss of membrane integrity, which consequently leads to failure in root functions, especially ion uptake, the major role played by ephemeral roots. Some of these electrolytes are likely to be amino acids, as reflected in the lower nitrogen concentrations at 35 °C, than lower temperatures (Fig. 9). Such a high temperature, which would rarely be sustained for days in moist soil in natural conditions, proved stressful for Concord grape roots.

Citrus roots (Bryla *et al.*, 2001) and Concord grape roots (Fig. 5A) tend to resume a homeostatic respiration rate after soil temperature rises above about 20 °C. This provides a mechanism to prevent roots from excessive carbon cost. The difference in respiratory response to temperature between citrus and Concord grape is due to the fact that the latter is less resistant to soil temperatures above 30 °C. The differences in high thermal tolerance in these two species are consistent with their differences in the climate of the species' origin.

Root acclimation to temperature only occurred at higher temperatures (Fig. 5). When soil temperature is shifted to low temperatures (<15 °C), root respiration remains low and does not exhibit homeostasis as in the case of temperature rise (Fig. 5B). Therefore, the tendency of root respiration to acclimate occurs when temperature is raised above the growth temperature but not when temperature is decreased. Similar results were observed in citrus (Bryla *et al.*, 2001). This phenomenon may be explained by factors limiting respiration (Atkin and Tjoelker, 2003). Under cool temperatures (<15 °C), root respiration is limited chiefly by enzyme capacity instead of by substrate and/or adenylate limitation. Many studies (Lunackova *et al.*, 2000; Covey-Crump *et al.*, 2002) show respiratory substrate (reducing sugars) increases in roots exposed to cold, which provides potential for a greater respiration increase when temperature rises. However, in the present study, sugar did not significantly accumulate in Concord grape root in cold soil (15 °C versus 25 °C and 35 °C). Since sugar is imported to the roots from the above-ground parts, there may be greater differences in sugar accumulation when whole root systems are exposed to low temperature. Carbohydrates may have been preferentially allocated to the warm roots with a higher metabolic activity outside the chambers.

Total root respiration is often partitioned into growth, ion-uptake, and maintenance (Veen, 1980; Bouma *et al.*, 1996). Because nutrients were not added to the sandy soil during the respiration measurements, ion uptake was minimized, which would be particularly the case in the drought experiments. Root growth undoubtedly occurred to some extent but its contribution during respiration measurements was likely to be small, as indicated by the fairly stable respiration rates at stable temperatures of 20 °C (Fig. 5B). Thus, most of the respiration observed was probably associated with maintenance respiration.

A decline in root respiration as soil dries has been observed in many plants (Palta and Nobel, 1989; Burton *et al.*, 1998; Huang and Fu, 2000; Maier and Kress, 2000; Bryla *et al.*, 2001). In citrus roots, respiration declined in a sigmoidal pattern with soil drying, retaining a basal level in very dry soil (Bryla *et al.*, 2001), which is consistent with this species tolerance of dry soil (Eissenstat *et al.*, 1999). In Concord grape roots, however, respiration declined logarithmically as soil became dry with no constant basal rate exhibited (Figs 6A, 8). Like high temperature, drought results in membrane breakdown in grape root cells (Fig. 6B) and reduced N concentrations, indicative of loss of amino acids (Fig. 9). Lower-order roots were more sensitive to drought than higher-order ones (Fig. 7). Therefore, when drought becomes more severe, roots will die back from lower order to higher order. A decrease in the respiration in grape roots exposed to drought is therefore not simply a result of reduced root growth and ion uptake (Espeleta and Eissenstat, 1998; Eissenstat *et al.*, 1999), but also of reduced maintenance costs associated with protein degradation, lower membrane potentials, and, eventually, root death.

At warmer temperatures, respiration declines faster and to a greater extent with soil drying than at cold temperatures (Fig. 8), suggesting grape roots exposed to higher temperatures are more responsive to drought. Because of temperature acclimation, there was little difference in respiratory response to soil moisture at 20 °C and 30 °C. At a low soil temperature (10 °C), Concord grape roots retained a basal level of respiration with depletion of soil moisture (Fig. 8), which is very similar to that observed in citrus (Bryla *et al*., 2001). Soil moisture also exerts influence on the response of respiration to temperatures in Concord grape root as Q_{10} appeared to drop with a reduction in soil moisture.

Modelling Concord grape root respiration to changes in soil temperature and moisture needs to include both the time-dependence of Q_{10}, growing temperature, and soil moisture. Similar to previous research in citrus, under moist soil conditions, a shift in temperature from 20 °C to 30 °C resulted in an increase in grape root respiration, which slowly decreased to a homeostatic level after several days. Unlike citrus, temperatures above 33 °C and soil moisture deficits led to a loss in tissue viability and increased electrolyte leakage. In citrus, Bryla *et al*. (2001) was able to model and predict respiration in the field with reasonable accuracy by taking the effects of acclimation to temperature as well as the effects of drought into account. Similar considerations are needed for Concord grape roots, although these predictions need to be tested under field conditions.

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