



Effect of different daytime and night-time temperature regimes on the foliar respiration of *Pinus taeda*: predicting the effect of variable temperature on acclimation

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Abstract

The objectives of this study were to determine the acclimation of loblolly pine (*Pinus taeda* L.) foliar respiration to different night-time low temperatures, daytime high temperatures, and daily mean temperatures, and then to use the responses of temperature acclimation to various temperature regimes to predict acclimation under fluctuating temperatures. Experiments were conducted on two-year-old seedlings in growth chambers using different combinations of day and night-time temperatures. The first experiment exposed trees to 22/22, 29/22, 22/15, and 29/15 °C day/night (d/n). When measured at a common temperature (15, 22 or 29 °C), respiration rates were lower for trees exposed to higher treatment temperatures and acclimation was influenced by both day and night-time temperature. However, the extent of acclimation did not relate to mean temperature, i.e. respiration rates measured at a common temperature ranked as follows for seedlings exposed to different temperature regimes, 22/15 > 22/22 > 29/15 ≈ 29/22 °C d/n. Rather, acclimation of foliar respiration was linearly related to mean daily respiration rate, where mean daily respiration rate is the average of the respiration rates measured at the day and night-time treatment temperatures. The discrepancy between mean daily respiration rate and mean daily temperature occurred because respiration increased exponentially with increasing temperature. In a second experiment, the same seedlings were exposed to 22/22, 15/15, 25.5/18.5, and 25.5/15 °C d/n to test the relationship between mean daily respiration rate and acclimation. As in the first experiment, acclimation was linearly related to mean daily respiration rate. The concept of effective

acclimation temperature, which is the temperature at which the mean daily respiration rate occurs, was derived from these results as a means to predict the extent that foliar respiration acclimates to treatment temperature.

Key words: Thermal acclimation, loblolly pine, *Pinus taeda* L., respiration, temperature.

Introduction

The temperatures that trees experience vary with daily and seasonal cycles and also vary between days with changing weather patterns. The short-term response of dark respiration of trees to these changes in temperature follows a Q_{10} response of approximately two (Teskey and Will, 1999; Tjoelker *et al.*, 1999a, b; Kozlowski *et al.*, 1991; Lambers, 1985). Superimposed on this short-term response is the thermal acclimation of dark respiration to shifts in temperature regime. Thermal acclimation of respiration occurs when exposure to higher temperatures decreases respiratory capacity, and is possibly due to decreased numbers of mitochondria (Miroslavov and Kravkina, 1991) or decreased respiratory capacity per mitochondria (Klikoff, 1966). The net effect is that when measured at a common temperature, trees exposed to higher temperature regimes have lower respiration rates than trees exposed to lower temperature regimes (Atkin *et al.*, 2000; Teskey and Will, 1999; Tjoelker *et al.*, 1999a, b; Paembonan *et al.*, 1991; Pereira *et al.*, 1986; Tranquillini *et al.*, 1986; Sorensen and Ferrell, 1973; Rook, 1969; Strain and Chase, 1966). This acclimation response can occur within several days (Atkin *et al.*, 2000; Rook, 1969).

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Experiments examining the acclimation of respiration of trees have employed temperature regimes with constant diurnal temperatures (Teskey and Will, 1999; Tranquillini *et al.*, 1986), regimes with a fixed difference between day and night temperatures (Tjoelker *et al.*, 1999a, b; Rook, 1969), or relied on uncontrolled seasonal temperature changes (Paembonan *et al.*, 1991; Pereira *et al.*, 1986; Strain and Chase, 1966). Although the results from previous experiments clearly show that respiration acclimates to temperature, little attempt has been made to determine the effect of daily temperature fluctuations on the extent of respiratory acclimation. For instance, respiration may acclimate to daytime high temperatures, night-time low temperatures, daily mean temperatures or some other aspect related to temperature regime. This question has important ramifications for predicting the respiration rates of trees growing in the field as temperature means and extremes fluctuate between days, seasons, and years, and differ across a species' range.

Prediction of the acclimation response of respiration to fluctuating temperature also has important implications for predicting the effects of global climate change. Given the impacts of higher temperature on respiratory carbon use and the countering effects of acclimation of respiration to temperature, understanding the effect of temperature acclimation to fluctuating temperature is imperative for predicting tree growth and productivity under various global climate change scenarios. Acclimation of respiration to temperature could offset the negative impacts on productivity of greater respiratory carbon use associated with warmer temperatures. However, if global warming results in warmer night-time or daytime temperatures only, and respiration acclimates to temperature extremes, acclimation may not dampen the effect of warmer temperatures on carbon use. For instance, if only night-time temperatures increase with global warming, and respiration acclimates to daytime temperatures, no acclimation will occur and more carbon will be used in respiration at night.

The objectives of this study were to determine the acclimation of loblolly pine (*Pinus taeda* L.) foliar respiration to different night-time low temperatures, daytime high temperatures and daily mean temperatures, and then to use the responses of temperature acclimation to various temperature regimes to predict acclimation under fluctuating temperatures. Two experiments were conducted. The first experiment tested the extent that respiration acclimates to night-time low temperature, daytime high temperature and mean daily temperature. The hypothesis was that respiration would acclimate to mean temperature. Potential outcomes of the first experiment were acclimation to night-time low temperature if similar respiration rates were measured at a common temperature for seedlings exposed to the same night-time temperature, acclimation to daytime high temperature if similar respiration rates were measured

at a common temperature for seedlings exposed to the same daytime temperatures, and acclimation to mean daily temperature if respiration rates were inversely related to mean daily temperature when measured at a common temperature.

The second experiment was designed to test hypotheses derived from the first experiment and to confirm and verify the results of the first experiment. The hypothesis tested was that acclimation of respiration is not a direct function of temperature. Rather, respiration measured at a common temperature is inversely related to the mean daily respiration rate. Mean daily respiration rate was defined as the average of the respiration rates measured at the day and night-time treatment temperatures for a given temperature regime. Results from both experiments were used to develop a relationship to predict the acclimation response to fluctuating temperatures.

Materials and methods

In February 1999, 1-year-old, bare root loblolly pine seedlings were planted, one tree per pot, in pots 7.0 l in size containing potting mix (Fafard 3B, Conrad Fafard Inc., Agawam, MA, USA). From the time of planting until the seedlings were moved to the growth chambers, the seedlings were kept in a greenhouse under ambient conditions, watered as needed, and fertilized on a weekly basis with an NPK plus micronutrient mix supplied as Miller Nutrileaf (Miller Chemical, Hanover, PA, USA) and also with chelated Fe (Miller Iron Chelate DP, Miller Chemical, Hanover, PA, USA). On 14 June 1999, eight seedlings were moved into each of four walk-in growth chambers (Environmental Growth Chambers, Chagrin Falls, OH) maintained at 22 °C, 50% relative humidity, and a 12 h light period. Light was supplied from a combination of incandescent and very high-output florescent bulbs such that photosynthetic photon flux density was approximately 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the top of the seedlings. While in the chambers, seedlings were watered as needed and fertilized weekly with the same nutrient mix that was used in the greenhouse. Seedlings were maintained in the chambers at constant temperature for 6 weeks before imposing temperature treatments. All seedlings were randomly assigned to new chambers at the beginning of the experiments.

Two experiments, one after the other, were conducted on the same seedlings. The first experiment tested whether respiration acclimated to night-time low temperature, daytime high temperature or mean daily temperature. The second experiment was used to confirm and verify the results of the first experiment and to determine the response of temperature acclimation to a larger range of temperature regimes. During both experiments, relative humidity was controlled in the chambers to keep VPD between 1.2 and 1.4 kPa. Throughout the experiment, the day/night period was 12/12 h. Every 3–4 d, seedlings were rotated between chambers with chambers reprogrammed to maintain the appropriate treatments.

The first experiment used treatments of 22/22, 29/22, 22/15, and 29/15 °C day/night temperature. Foliar dark respiration was measured with a LI-6400 portable photosynthesis system (Li-Cor Inc., Lincoln NE, USA) at 15, 22, and 29 °C 7 d and 17 d after imposing the temperature treatments at a CO_2 concentration of 370 $\mu\text{mol mol}^{-1}$. Seedlings were exposed to the measurement temperatures for a minimum of 1 h before the

measurements. The cuvette was used to control leaf temperature precisely. The same three fascicles per tree were measured at all three temperatures. Fully expanded fascicles were measured to eliminate the effects of growth respiration. Measurements were conducted towards the end of the dark period. Respiration was measured over 5 d, such that a seedling was measured every other day at one temperature. The order of measurement temperature was randomized as was the chamber in which the seedlings were measured. At the completion of the second measurement cycle, fascicles were removed, their specific leaf area determined, and their nitrogen concentration determined using a NC2100 CNS analyser (CE Elantech, Inc., Lakewood NJ, USA).

Because the respiration rates of the different treatments had not changed between the first and second sampling periods (days 7 and 17), acclimation was considered to be complete and the seedlings were randomly placed into new groups and new temperature regimes for the second experiment. The temperature regimes of the second experiment were 22/22, 15/15, 25.5/18.5, and 25.5/15 °C d/n temperature. After 16 d at the new temperature regimes, dark respiration of seedlings was measured at 22 °C.

When seedlings were measured at more than one temperature in the first experiment, a repeated measures analysis of variance was conducted to determine the significance of the between-subject effect of treatment temperature and the within-subject effect of measurement temperature. When a treatment temperature \times measurement temperature interaction was significant in the first experiment, the effect of treatment temperature on respiration was further examined by testing its significance at each measurement temperature. Analysis of variance was used to determine the significance of specific leaf area and foliar nitrogen concentration in the first experiment as well as when seedlings were measured at only one temperature during the second experiment. Means separation procedures were conducted using Duncan's multiple range test.

Results

Dark respiration measurements of seedlings from the different treatment temperatures after 7 d of exposure were similar to those measured after 17 d of exposure indicating that acclimation was complete after 1 week. Because of the similarity between the two sampling dates, the discussion of the results will focus on the measurements made after 17 d of exposure. When measured at 15, 22, and 29 °C after 17 d of exposure to the treatment temperatures, there was a significant effect of treatment temperature ($P < 0.0001$), a significant effect of measurement temperature ($P < 0.0001$), and a significant treatment \times measurement temperature interaction ($P < 0.0009$). Respiration rates increased with increasing measurement temperature. For all treatments, respiration increased approximately 2.5 times over the 14 °C increase in temperature from 15 °C to 29 °C (Fig. 1). Overall, the respiration rates of the 22/15 d/n treatment seedlings were significantly greater than the rates of seedlings from the other treatments, the respiration rates of the 22/22 d/n treatment seedlings were significantly greater than seedlings in the 29/15 d/n and the 29/22 d/n treatments,

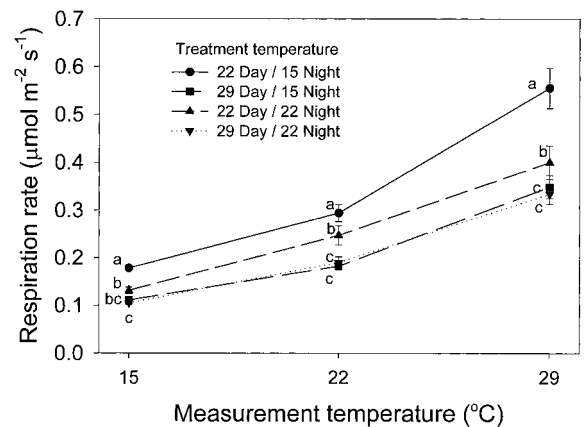


Fig. 1. Respiration rates of the seedlings exposed to different temperature regimes measured at three different temperatures. Error bars represent the standard error of the mean. Different letters within a measurement temperature indicate significant differences ($P < 0.05$).

and the respiration rates of the seedlings from the 29/15 d/n and 29/22 d/n treatments were similar (Fig. 1). When each measurement temperature was analysed separately, this pattern was statistically significant at both 22 °C and 29 °C measurement temperatures ($22/15 > 22/22 > 29/15 \approx 29/22$ d/n) (Fig. 1). At 15 °C measurement temperature, the pattern was the same, but the 22/22 d/n treatment was not significantly different from the 29/15 d/n treatment (Fig. 1).

From the results shown in Fig. 1, respiration acclimated to a combination of daytime and night-time temperature that was not equal to the mean temperature. Night-time low temperatures affected acclimation because seedlings exposed to 22/15 d/n temperatures had higher respiration rates than seedlings exposed to constant 22 °C temperature. Daytime high temperatures also affected acclimation because seedlings exposed to 29/22 d/n temperatures had lower respiration rates than seedlings exposed to constant 22 °C temperature. However, seedlings in the 29/15 d/n treatment had respiration rates that were significantly lower than seedlings in the 22/22 d/n treatment even though the 29/15 d/n temperature regime had the same mean temperature as the constant 22 °C treatment.

From the acclimation response observed in this experiment, the concept of *effective acclimation temperature* was derived. The effective acclimation temperature is the temperature at which the mean daily respiration rate occurs (Fig. 2). The effective acclimation temperature and the mean daily temperature differ because of the exponential relationship between respiration and measurement temperature. Using this concept, effective acclimation temperatures were calculated for the four treatments using the Q_{10} response for each particular treatment. The overall respiration rate (mean of the respiration rates for a treatment measured at 15, 22 and 29 °C) was plotted

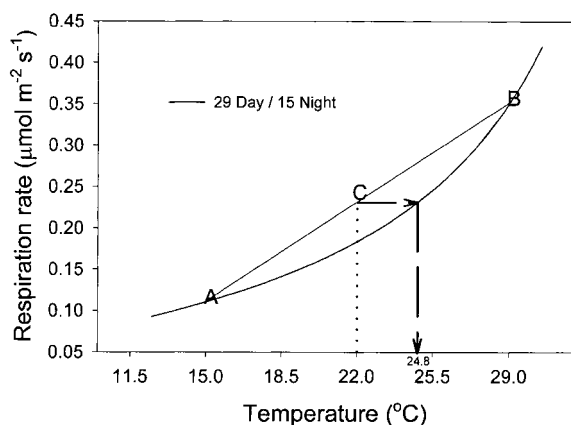


Fig. 2. Calculation of effective acclimation temperature for 29/15 day/night exposed seedlings using the measured Q_{10} response for this treatment. Point A is night-time respiration rate. Point B is daytime respiration rate. Point C is the mean daily respiration rate. Effective acclimation temperature is the temperature at which the mean daily respiration rate occurs (24.8 °C).

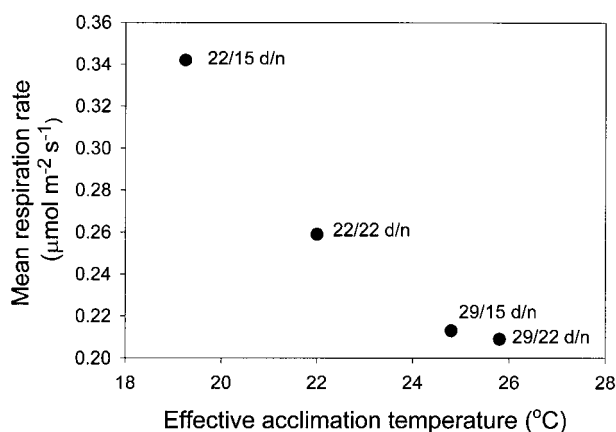


Fig. 3. Relationship between the calculated effective acclimation temperature and the mean of the respiration rates measured at 15, 22, and 29 °C of the seedlings exposed to different treatment temperatures. Treatment temperatures are listed next to the points on the graph.

against the effective acclimation temperature and the relationship was fairly linear (Fig. 3). Using the concept of effective acclimation temperature, the respiration rate (measured at a common temperature) of seedlings in the 29/15 d/n would be expected to be lower than the seedlings in the 22/22 d/n treatment and almost the same as the seedlings in the 29/22 d/n treatment (Fig. 3).

Temperatures for the second experiment were chosen to test the concept of effective acclimation temperature. The 22/22 d/n treatment was chosen for comparisons within and between experiments and the 15/15 d/n treatment was chosen to see if an effective acclimation temperature of 15 °C resulted in respiration rates that were greater and linearly related to the other respiration rates when plotted at their effective acclimation temperatures. Using a Q_{10} curve derived from the mean response of all treatments in the first experiment, 25.5/15 d/n was

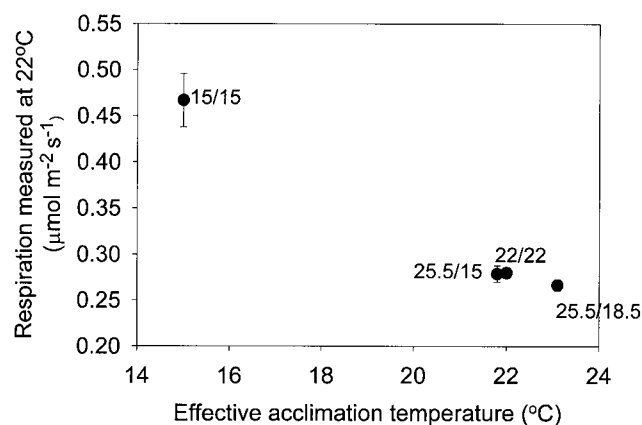


Fig. 4. Relationship between respiration rates measured at 22 °C and the calculated effective acclimation temperature for the seedling when exposed to new temperatures during the second experiment. Error bars represent standard error of the mean. Treatment temperatures are listed next to the points on the graph.

chosen to achieve an effective acclimation temperature approximately equal to the 22 °C, and 25.5/18.5 d/n was chosen to achieve an effective acclimation temperature greater than 22 °C, but less than those resulting from the 29/15 d/n and 29/22 d/n treatments in the first experiment.

As with the first experiment, there was a linear relationship between effective acclimation temperature and respiration measured at a common temperature in the second experiment (Fig. 4). In addition, respiration rate was much better related to effective acclimation temperature than mean temperature. If respiration rates were dependent on mean temperature, then the seedlings in the 25.5/18.5 d/n treatment (mean temperature 22 °C) would have respiration rates similar to seedlings in the 22/22 d/n treatment and the seedlings in the 25.5/15 d/n treatment (mean temperature 20.25 °C) would have respiration rates greater than those in the 22/22 d/n treatment. Instead, the respiration rates measured at 22 °C reflect the effective acclimation temperatures. The 25.5/18.5 d/n treatments (effective acclimation temperature 23.1 °C) had rates lower than the 22/22 d/n treatment and the 25.5/15 d/n treatment (effective acclimation temperature 21.8 °C) had rates similar to those of the 22/22 d/n treatment. Although the respiration rates from the first experiment are generally lower than those in the second experiment, a clear linear relationship is apparent when the results of both experiments are combined (Fig. 5).

The treatment temperature regimes did not significantly affect nitrogen concentration. Nitrogen concentrations at the end of the first experiment were 21.4, 20.7, 19.9, and 19.7 mg g⁻¹ for the 22/15, 29/22, 22/22, and 29/15 d/n treatments, respectively. Thus, there was not a significant effect of treatment temperature on nitrogen concentration that corresponded to the significant treatment effect on respiration rate. However, the slope of the relationship between respiration rate measured at

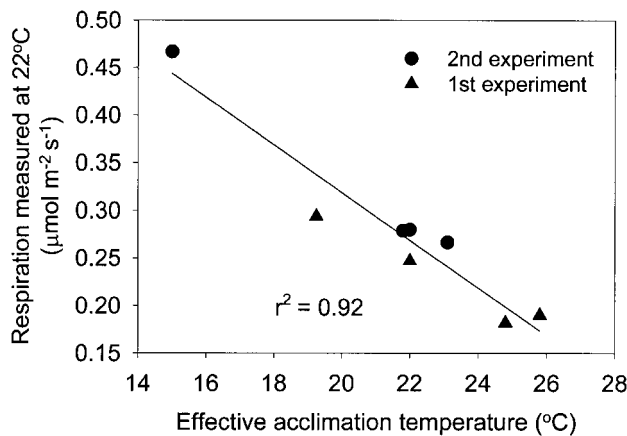


Fig. 5. Relationship between respiration rate measured at 22 °C and the calculated effective acclimation temperature for both experiments combined.

22 °C and fascicle nitrogen concentration was significant ($P < 0.0043$, $r^2 = 0.25$) indicating that for individual seedlings, respiration rate of fascicles was related to fascicle nitrogen concentration (Fig. 6). Similar results were obtained for regressions of nitrogen concentration and respiration rates measured at 15 °C and 29 °C.

Specific leaf area ($\text{m}^2 \text{kg}^{-1}$) was not significantly different between seedlings exposed to the different treatment temperatures. However, there was a slight trend towards lower specific leaf area with cooler treatment temperature. When respiration was expressed on a leaf weight basis instead of a leaf area basis, the differences between treatments were slightly less, but neither the treatment rankings nor the significance of the differences between treatments were affected.

Discussion

Acclimation of foliar respiration was linearly related to mean daily respiration rate, not mean temperature. Mean daily respiration rate refers to the average of the respiration rates that occurs at the day and night-time treatment temperatures. The difference between mean daily respiration rate and mean temperature is due to the exponential shape of the Q_{10} response and as a result, is larger as Q_{10} increases or the variation in temperature increases. However, since both respiration rate and acclimation were similarly related to temperature in a non-linear fashion, the relationship between acclimation and mean daily respiration rate was linear. Whether there is a causal relationship between mean daily respiration rate and acclimation can not be determined from these experiments. However, it is possible that acclimation may occur in response to the daily carbon use.

This direct relationship between mean daily respiration and the extent of acclimation provides a way to predict acclimation using effective acclimation temperature.

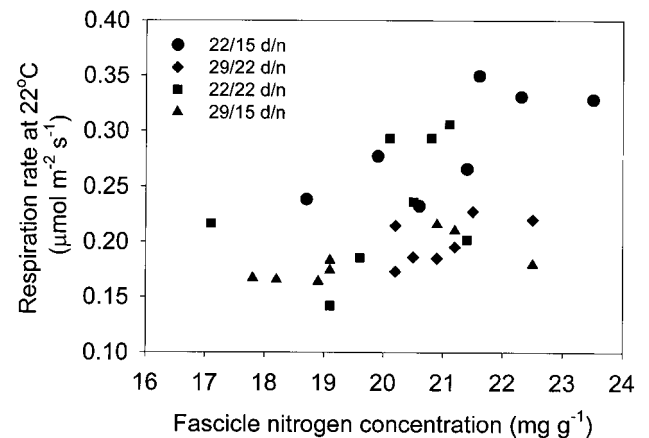


Fig. 6. Relationship between fascicle nitrogen concentration and respiration rate measured at 22 °C at the end of the first experiment. Each point is an individual seedling.

Effective acclimation temperature is calculated as the temperature at which the mean daily respiration rate occurs. Although effective acclimation temperature is an artificial construct, it serves as a surrogate for mean daily respiration rate and allows prediction of acclimation under different temperature regimes. The power and benefit of using effective acclimation temperature to predict acclimation to new temperature regimes is that prediction is possible without knowing specific rates of respiration as long as a Q_{10} response is measured or assumed. Although Q_{10} may change with changing growth temperature, assuming a Q_{10} of approximately 2.0 is acceptable for estimation in most cases as this has been the approximate Q_{10} found in numerous studies for a wide range of tree species and conditions (Teskey and Will, 1999; Tjoelker *et al.*, 1999a, b; Kozłowski *et al.*, 1991; Lambers, 1985). Once a Q_{10} has been established, the effective acclimation temperature under a new temperature regime can be calculated by determining the average daily respiration rate in relative units and then calculating where along the Q_{10} response curve that this respiration rate occurs (Fig. 2). Once the effective acclimation temperature has been calculated, the shift in respiration due to acclimation can be calculated from the relationship between effective acclimation temperature and respiration measured at a common temperature. For this experiment with loblolly pine seedlings, this relationship was linear with a slope of $-0.025 \mu\text{mol m}^{-2} \text{s}^{-1} \text{°C}^{-1}$ (Fig. 5).

Using effective acclimation temperature to predict the effect of new temperature regimes on respiration provides a basis to model the effect of different temperature scenarios on carbon use and productivity. Although the experiments in this study incorporated a level of complexity not previously examined in the context of acclimation, they were rudimentary compared to the complexity of temperature and environmental variation that occurs in the field. Further research needs to be conducted to verify

that the concept of effective acclimation temperature holds up in the field. For instance, the slope, and perhaps the shape, of the relationship between effective acclimation temperature and respiration at a common temperature will be species specific, and may be influenced by nutrition, phenology or interactions with environmental factors other than temperature. However, the results of this experiment are very promising and provide evidence that the extent of loblolly pine acclimation was predictable under different temperature regimes.

Although the range of day and night temperatures were limited in this study by the number of chambers, the results appear to be robust. Two experiments conducted a month apart resulted in similar relationships between effective acclimation temperature and respiration at a common temperature. In addition, after the completion of the experiments, the same trees were measured after acclimation to 27/17 d/n and 17/27 d/n to determine whether the response to treatment temperature was dependent on the diurnal pattern of temperatures. There was no difference between the treatments in respiration measured at a common temperature indicating that even with this extreme example, the concept of effective acclimation temperature was applicable regardless of when high and low temperatures occurred.

In this study, the respiration rates from the first experiment were slightly lower than those from the second experiment, i.e. the 22/22 d/n treatment was lower in the first experiment. There are several possible reasons for this including slight changes between the two experiments in foliar nutrient status, phenology, source/sink dynamics or carbohydrate status. Even with baseline changes in respiration rate, the concept of effective acclimation temperature is still valid to predict relative changes in acclimation because it is based on the slope of the relationship between effective acclimation temperature and respiration at a common temperature.

Tjoelker *et al.* found that foliar respiration of five boreal tree species measured at 18 °C was linearly related to foliar nitrogen concentration and total non-structural carbohydrate concentration (TNC) (Tjoelker *et al.*, 1999b). Foliar nitrogen concentration decreased with increasing growth temperature in three coniferous species they measured and they attributed the change to metabolic adjustment in response to thermal environment. The nitrogen response they found was similar to the relationship between nitrogen concentration, growth temperature and respiration rate found in this study. The slight, non-significant decrease in this study and the decrease found by Tjoelker *et al.* (Tjoelker *et al.*, 1999b), in nitrogen concentration for plants grown under warmer temperatures did not occur as a result of dilution associated with increased TNC or decreased specific leaf areas. Rather, nitrogen concentration probably increased

in cold-acclimated plants due to an increase in protein levels (Graham and Patterson, 1982).

In this study, all measurements of respiration were made on fully mature foliage of trees of similar phenological stages towards the end of the dark period. Depending on the species, the study, and the growth conditions, a diurnal pattern of foliar dark respiration may (Noguchi *et al.*, 1996; Irving and Silsbury, 1988; Breeze and Elston, 1978) or may not occur (Noguchi *et al.*, 1996; Irving and Silsbury, 1988) whereby respiration decreases during the night. This decrease is probably related to decreased phloem loading and carbon export as soluble sugar concentration decreases in the foliage (Noguchi *et al.*, 1996; Bouma *et al.*, 1995; Breeze and Elston, 1978). As such, dark respiration could be affected by different rates of photosynthate export under different night-time temperatures or by different rates of photosynthesis during the day. In this study, lower respiratory capacity of the seedlings grown in warmer temperature regimes was not driven by a depletion of soluble sugars during the dark period since respiration rates were different between seedlings grown in temperature regimes with the same night-time temperature, i.e. the 22/15 d/n and the 29/15 d/n treatments. Similarly, irradiance in the chambers was constant and leaf area-based measurements of photosynthesis were not significantly affected by temperature regime (data not shown) indicating that there were not large differences in carbon supply between seedlings exposed to the different treatments. Given this evidence, it is reasonable to assume that the thermal acclimation of respiration in this study was in large part controlled by changes in the capacity of maintenance respiration.

The results of this study indicate that acclimation of foliar respiration to temperature was correlated to mean daily respiration rate and that the extent of acclimation can be predicted by effective acclimation temperature using an estimated Q_{10} response. Although more research is necessary, this study begins to explain acclimation of respiration to fluctuating temperature and provides a basis to conceptualize and predict the response.

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References

- Atkin OK, Holly C, Ball MC. 2000. Acclimation of snow gum (*Eucalyptus pauciflora*) leaf respiration to seasonal and diurnal variations in temperature: the importance of changes in the capacity and temperature sensitivity of respiration. *Plant, Cell and Environment* **23**, 15–26.
- Bouma TJ, De Visser R, Van Leeuwen PH, De Kock MJ, Lambers H. 1995. The respiratory energy requirements

- involved in nocturnal carbohydrate export from starch-storing mature source leaves and their contribution to leaf dark respiration. *Journal of Experimental Botany* **46**, 1185–1194.
- Breeze V, Elston J.** 1978. Some effects of temperature and substrate content upon respiration and carbon balance of field beans (*Vicia faba* L.). *Annals of Botany* **42**, 863–876.
- Graham D, Patterson BD.** 1982. Responses to low, non-freezing temperatures: proteins, metabolism, and acclimation. *Annual Review of Plant Physiology* **33**, 347–372.
- Irving DE, Silsby JH.** 1988. The respiration of mature field bean (*Vicia faba* L.) leaves during prolonged darkness. *Annals of Botany* **62**, 473–479.
- Klikoff LC.** 1966. Temperature dependence of the oxidative rates of mitochondria in *Danthonia intermedia*, *Penstemon davidsonii* and *Sitanion hystrix*. *Nature* **212**, 529–530.
- Kozlowski TT, Kramer PJ, Pallardy SG.** 1991. *The physiological ecology of woody plants*. New York: Academic Press.
- Lambers H.** 1985. Respiration in intact plants and tissues: its regulation and dependence on environmental factors, metabolism and invaded organisms. In: Douce R, Day DA, eds. *Encyclopedia of plant physiology*, New series, Vol. 18. *Higher plant cell respiration*. New York: Springer-Verlag, 418–473.
- Miroslavov EA, Kravkina IM.** 1991. Comparative analysis of chloroplasts and mitochondria in leaf chlorenchyma from mountain plants grown at different altitudes. *Annals of Botany* **68**, 195–200.
- Noguchi K, Sonoike K, Terashima I.** 1996. Acclimation of respiratory properties of leaves of *Spinacia oleracea* L., a sun species, and of *Alocasia macrorrhiza* (L.) G. Don., a shade species, to changes in growth irradiance. *Plant Cell Physiology* **37**, 377–384.
- Paembonan SA, Hagiwara A, Hozumi K.** 1991. Long-term measurement of CO₂ release from above-ground parts of a hinoki forest tree in relation to air temperature. *Tree Physiology* **8**, 399–405.
- Pereira JS, Tenhunen JD, Lange OL, Beyschlag W, Meyer A, David MM.** 1986. Seasonal and diurnal patterns in leaf gas exchange of *Eucalyptus globulus* trees growing in Portugal. *Canadian Journal of Forest Research* **16**, 177–184.
- Rook DA.** 1969. The influence of growing temperature on photosynthesis and respiration of *Pinus radiata* seedlings. *New Zealand Journal of Botany* **7**, 43–55.
- Sorensen FC, Ferrell WK.** 1973. Photosynthesis and growth of Douglas-fir seedlings when growth in different environments. *Canadian Journal of Botany* **51**, 1689–1698.
- Strain BR, Chase VC.** 1966. Effect of past and prevailing temperatures on the carbon dioxide exchange capacities of some woody desert perennials. *Ecology* **47**, 1043–1045.
- Teskey RO, Will RE.** 1999. Acclimation of loblolly pine (*Pinus taeda*) seedlings to high temperatures. *Tree Physiology* **19**, 519–525.
- Tjoelker MG, Oleksyn J, Reich PB.** 1999a. Acclimation of respiration to temperature and CO₂ in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biology* **49**, 679–691.
- Tjoelker MG, Reich PB, Oleksyn J.** 1999b. Changes in leaf nitrogen and carbohydrates underlie temperature and CO₂ acclimation of dark respiration in five boreal tree species. *Plant, Cell and Environment* **22**, 767–778.
- Tranquillini W, Havranek WH, Ecker P.** 1986. Effects of atmospheric humidity and acclimation temperature on the temperature responses of photosynthesis in young *Larix decidua* Mill. *Tree Physiology* **1**, 37–45.