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The hot and the cold: unravelling the variable response of plant respiration to temperature

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This paper is part of The Evans Review series, named for Dr Lloyd Evans. The series contains reviews that are critical, state-of-the-art evaluations that aim to advance our understanding, rather than being exhaustive compilations of information, and are written by invitation.

Abstract. When predicting the effects of climate change, global carbon circulation models that include a positive feedback effect of climate warming on the carbon cycle often assume that (1) plant respiration increases exponentially with temperature (with a constant Q_{10}) and (2) that there is no acclimation of respiration to long-term changes in temperature. In this review, we show that these two assumptions are incorrect. While Q_{10} does not respond systematically to elevated atmospheric CO_2 concentrations, other factors such as temperature, light, and water availability all have the potential to influence the temperature sensitivity of respiratory CO_2 efflux. Roots and leaves can also differ in their Q_{10} values, as can upper and lower canopy leaves. The consequences of such variable Q_{10} values need to be fully explored in carbon modelling. Here, we consider the extent of variability in the degree of thermal acclimation of respiration, and discuss in detail the biochemical mechanisms underpinning this variability; the response of respiration to long-term changes in temperature is highly dependent on the effect of temperature on plant development, and on interactive effects of temperature and other abiotic factors (e.g. irradiance, drought and nutrient availability). Rather than acclimating to the daily mean temperature, recent studies suggest that other components of the daily temperature regime can be important (e.g. daily minimum and / or night temperature). In some cases, acclimation may simply reflect a passive response to changes in respiratory substrate availability, whereas in others acclimation may be critical in helping plants grow and survive at contrasting temperatures. We also consider the impact of acclimation on the balance between respiration and photosynthesis; although environmental factors such as water availability can alter the balance between these two processes, the available data suggests that temperature-mediated differences in dark leaf respiration are closely linked to concomitant differences in leaf photosynthesis. We conclude by highlighting the need for a greater process-based understanding of thermal acclimation of respiration if we are to successfully predict future ecosystem CO_2 fluxes and potential feedbacks on atmospheric CO_2 concentrations.

Keywords: carbon fluxes, climate change, respiration, temperature.

Introduction

Mitochondrial respiration plays a pivotal role in determining the growth and survival of plants, and has a profound impact on net ecosystem CO_2 exchange and the concentration of CO_2 in the atmosphere (Gifford 2003). Much of the energy and carbon skeletons necessary for biosynthesis and cellular maintenance are produced by plant respiration. Under some conditions (e.g. excess irradiance), respiration (R) may also help minimise the formation of potentially damaging reactive oxygen species (ROS) through oxidation of excess cellular

Abbreviations used: AOX, alternative oxidase; GCMs, global circulation models; OAA, oxaloacetate; P, photosynthesis; P_{sat}, light-saturated photosynthesis; PUMP, plant uncoupling mitochondrial proteins; Q_{10}, proportional change in respiration with a 10°C increase in temperature; R, respiration; ROS, reactive oxygen species; V_{max}, maximum velocity used in Michaelis–Menten kinetics.

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redox equivalents (Saradadevi and Raghavendra 1992; Shyam *et al*. 1993; Purvis and Shewfelt 1993; Hurry *et al*. 1995; Maxwell *et al*. 1999). *R* is also crucial for (1) the production of ascorbate (vitamin C; Millar *et al*. 2003), a necessary component of the protective xanthophyll and glutathinone cycles, (2) the maintenance of photosynthetic activity, largely because of the energy demands of sucrose synthesis (Krömer 1995), and (3) regulating pathogen defence processes (Noctor *et al*. 2004). *R* also plays an important role in determining the carbon budget of individual plants and the concentration of CO_2 in the atmosphere. Between 30 and 80% of the CO_2 taken up by photosynthesis (*P*) each day is subsequently respired (Poorter *et al*. 1990; Atkin *et al*. 1996; Tjoelker *et al*. 1999*a*; Amthor 2000; Loveys *et al*. 2002). Thus, plant *R* contributes up to 65% of the total CO_2 released into the atmosphere at the ecosystem level; with the remaining CO_2 being derived from heterotrophic soil *R* (Xu *et al*. 2001; Reichstein *et al*. 2002). Globally, plant *R* releases approximately 60 Gt of carbon into the atmosphere each year. Although largely balanced by carbon uptake through photosynthesis, annual respiratory carbon flux to the atmosphere is approximately ten times the CO_2 released by fossil fuel burning (Raich and Schlesinger 1992; Amthor 1997; Field 2001). However, the extent of respiratory CO_2 release may change in the future in response to global climate change. Coupled climate and carbon cycle models need to incorporate variability in rates of plant *R* if they are to accurately predict future atmospheric CO_2 concentrations.

One of the most important environmental parameters affecting rates of plant *R* is temperature (James 1953; Forward 1960; Berry and Raison 1981). It is often assumed that the relationship between plant *R* and temperature is exponential with a constant Q_{10} (i.e. proportional change in *R* with a 10°C increase in temperature, typically around 2) (e.g. Atkin and Day 1990; Ryan 1991; Raich and Schlesinger 1992). As a result, most simulation models such as Biome-BGC, Century (Schimel *et al*. 1997), PnET (Aber and Federer 1992) and several dynamic vegetation models (White *et al*. 2000; Cramer *et al*. 2001) assume that *R* responds to short- and long-term changes in temperature in a fixed, exponential manner ($Q_{10} = 2.0$). Based on such assumptions, coupled global circulation models (GCMs) predict that global warming will result in increased rates of respiratory CO_2 efflux into the atmosphere, which in turn will compound the greenhouse effect. For example, mean annual land surface air temperatures are predicted to be 2.5°C higher by the year 2100 in positive feedback models that incorporate the effects of increased respiratory CO_2 efflux than in models that do not include a feedback component (Cox *et al*. 2000). In the Cox *et al*. (2000) coupled model, it is also assumed that *R* will not acclimate to long-term changes in temperature (i.e. rates of *R* at a given measurement temperature remain constant over time). However, there is growing evidence that the response of *R* to temperature is dynamic, with plant *R* often acclimating

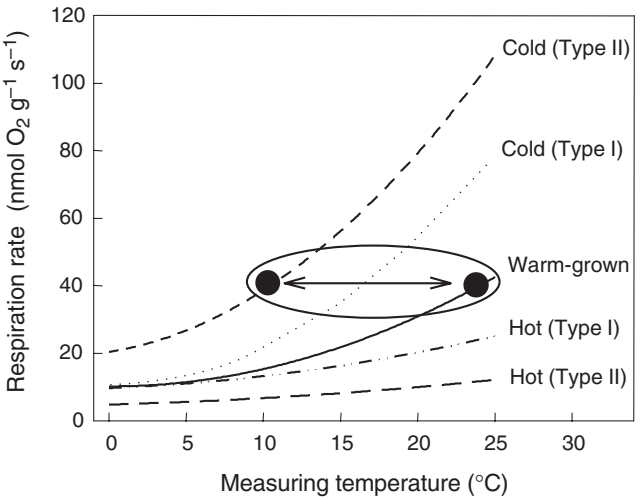

Fig. 1. Diagrammatic representation of the temperature response of respiration in warm-grown plants and plants acclimated to cooler and hotter temperatures. In Cold (Type I) and Hot (Type I), respiration rates are similar to those of the warm-grown plants when measured at low temperatures (e.g. less than 5°C). However, large differences are observed in rates of *R* at higher measuring temperatures (i.e. the Q_{10} increases and decreases following cold- and hot-acclimation, respectively). In Cold (Type II) and Hot (Type II), differences in rates of *R* are observed at both low and high measuring temperatures. The horizontal arrow highlights near homeostasis in rates exhibited by the warm-grown and cold-acclimated (Type II) counterparts, when each are measured at their respective growth temperatures. A summary of the two types of acclimation (Type I and Type II) is given the in text. A more detailed account is provided by Atkin and Tjoelker (2003).

to long-term changes in temperature (Fig. 1). Moreover, neither Q_{10} values nor degrees of acclimation are constant; rather, both vary in response to the surrounding environment and / or the metabolic status of the plant. Consequently, GCMs that fail to take into account such variability in Q_{10} and degrees of temperature acclimation of *R* are likely to result in large over-estimates of annual respiratory CO_2 release into the atmosphere (e.g. Fig. 2; Atkin *et al*. 2000*a*; Wythers *et al*. 2005) and consequently over-estimate the extent to which atmospheric CO_2 concentrations will rise over long periods (Luo *et al*. 2001). The importance of understanding variability in the Q_{10} is highlighted by predicted changes in the amplitude of diurnal temperatures experienced by plants (e.g. nights are increasing to a greater extent than day time temperatures; Easterling *et al*. 1997).

Although recent reviews have considered aspects of the temperature response of plant *R*, focussing on roots in Atkin *et al*. (2000*a*) and the mechanisms responsible for variability in Q_{10} values in Atkin and Tjoelker (2003), no review has yet provided a detailed account of the extent of variability in Q_{10} values in both leaves and roots under various environmental conditions, or focussed on biochemical mechanisms underpinning variability in the degree of temperature acclimation. The current review discusses these issues in detail, starting with variability in

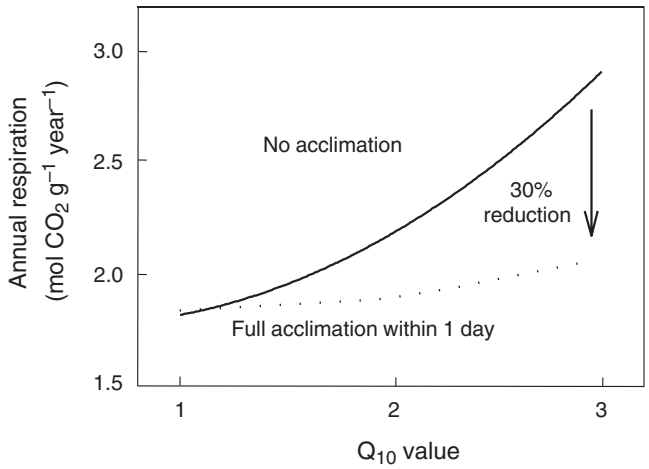

Fig. 2. Theoretical example of the impact of acclimation and Q_{10} values on annual respiratory CO_2 release by plant tissues. Based on temperature data recorded by Atkin *et al*. (2000*b*), using the assumptions outlined by Atkin *et al*. (2000*a*). In this model, annual CO_2 release is 47% higher in tissues with a Q_{10} of 3.0 compared with that of tissues with a Q_{10} of 1.5, whereas rapid acclimation reduced annual CO_2 release by up to 40%. Moreover, acclimation markedly decreases annual respiratory CO_2 release, particularly in plant tissues exhibiting high Q_{10} values.

the short- and long-term temperature response of leaf and root respiration. It then addresses the question of whether thermal acclimation represents a passive response to changes in respiratory substrate supply and / or an active process to provide the energy necessary for growth and maintenance processes following large changes in growth temperature and / or protect plants against oxidative damage. Finally, the impact of acclimation on the balance between *R* and *P* is considered. Although our review does not consider the direct and indirect effects of atmospheric CO_2 concentration on plant *R* per se [see Gonzàlez-Meler *et al*. (2004) for thorough review of this topic], we do consider the effects of growth CO_2 concentration on the Q_{10} of leaf *R*. For a recent review of how plant respiration is represented in terrestrial carbon models see Gifford (2003).

Variation in the Q_{10} of respiration

To what extent does the Q_{10} of leaf and root *R* vary? Here, we show that although atmospheric CO_2 concentration influences the Q_{10} of *R* in some studies, a survey of literature indicates that growth CO_2 concentration does not, on average, increase Q_{10} values. The Q_{10} of leaf *R* is often, but not always, reduced in the light compared with the Q_{10} of leaf *R* in the dark. Q_{10} values are often lower in water-stressed plants than in their fully-watered counterparts. Roots and leaves can also differ in their Q_{10} values, as can upper and lower canopy leaves. Q_{10} of both root and leaf *R* dark generally decrease with increasing measurement temperature. The assumption that Q_{10} values are constant and equal to 2.0 is not, therefore, supported by the literature. As such, the consequences of variable Q_{10} values (*v.* using a fixed Q_{10} of 2.0) need to be fully explored in carbon modelling.

Atmospheric CO_2 concentration

Growth CO_2 concentration does not appear to have a predictable, systematic effect on the Q_{10} of dark respiration of leaves, stems, or roots (Table 1). The effect of atmospheric CO_2 concentration during growth on Q_{10} values of *R* measured in darkness for above and below ground organs differs among studies, increasing by more than 10% in 14 of the cases shown in Table 1, decreasing by more than 10% in seven cases, or remaining unchanged (i.e. change less than 10%) in 34 cases; overall, elevated CO_2 had little impact on the average Q_{10} values shown in Table 1. Nevertheless, there are cases where the Q_{10} of dark respiration is greater in plants grown under elevated atmospheric CO_2 concentration. For example, Shapiro *et al*. (2004) found that growth under elevated CO_2 increased both $Q_{10\,/\,dark}$ (Table 1) and $Q_{10\,/\,light}$ values of leaf respiration in *Xanthium strumarium*. Moreover, Q_{10} values also increased by elevated CO_2 in late stage of needle expansion in *Pinus sylvestris* (Zha *et al*. 2001) [but see Zha *et al*. (2005) for contrasting results]. Overall, however, the literature results suggest that growth CO_2 concentration does not on average alter the temperature sensitivity of dark respiration in roots, leaves, or shoots, among the studies shown in Table 1.

Water and nutrient availability

In the short term, water stress results in a reduction in leaf and root *R*. Root *R* declines during drought (Bryla *et al*. 1997, 2001; Burton *et al*. 1998). Under field conditions the relationship between soil drying and root *R* is often further complicated with occurrence of increased soil temperatures during drought. However, in a greenhouse study in which roots of citrus trees were maintained at constant temperatures, root *R* declined with decreasing soil water content over a 10-d drying period (Bryla *et al*. 2001). In addition, drought-induced reductions in root *R* were greater in warmer soils (25 and 35°C) than in a cooler soil (15°C) as soil water contents fell below 6%. Comparing the proportional differences in *R* at the three soil temperatures suggests that Q_{10} declined concurrently with soil drying. Moreover, this study demonstrated that root *R* acclimated to both soil moisture and soil temperatures (>23°C).

Although leaf *R* declines in response to short-term water deficits, less is known concerning the effects of long-term water deficits on respiratory function and Q_{10}. In a study of three deciduous tree species growing in two sites of contrasting water availability, Q_{10} differed amongst species (1.5–2.1) and was lower at the drier than the wetter site (Turnbull *et al*. 2001). In addition, both area- and mass-based leaf *R* were higher and light-saturated rates of *P* lower at the drier than at the wetter site, suggesting that leaf-level net carbon gain was reduced at the dry site. These findings

Table 1. Published values of Q_{10} of dark respiration of plants grown and measured under ambient or elevated atmospheric CO_2 concentration

See individual references for details on the concentrations of atmospheric CO_2 used. Values of Q_{10} were obtained from published sources or derived from temperature functions of respiration and / or from table values of both temperature and respiration rates

Species	Organ	Atmospheric CO_2 concentration		Comment	Reference
		Ambient	Elevated		
Xanthium strumarum	leaf	2.00	3.37	High N	Shapiro *et al.* (2004)
Xanthium strumarum	leaf	1.94	3.00	Low N	Shapiro *et al.* (2004)
Gossypium hirsutum	leaf	3.19	2.78		Harley *et al.* (1992)
Pinus sylvestris	shoot	1.93	2.03	May	Zha *et al.* (2003)
Pinus sylvestris	shoot	1.80	1.75	June	Zha *et al.* (2003)
Pinus sylvestris	shoot	1.67	1.79	July	Zha *et al.* (2003)
Pinus sylvestris	shoot	1.75	1.93	August	Zha *et al.* (2003)
Pinus sylvestris	shoot	2.03	2.18	September	Zha *et al.* (2003)
Pinus sylvestris	shoot	2.10	2.25	October	Zha *et al.* (2003)
Pinus sylvestris	needle	2.08	2.06	Early stage of needle expansion	Zha *et al.* (2001)
Pinus sylvestris	needle	2.09	2.32	Late stage of needle expansion	Zha *et al.* (2001)
Populus tremuloides	shoot	1.88	1.81	Growth temperature 18 / 12°C	Tjoelker *et al.* (1999*b*)
Populus tremuloides	shoot	1.82	1.89	Growth temperature 24 / 18°C	Tjoelker *et al.* (1999*b*)
Populus tremuloides	shoot	1.77	1.79	Growth temperature 30 / 24°C	Tjoelker *et al.* (1999*b*)
Betula papyrifera	shoot	2.19	2.16	Growth temperature 18 / 12°C	Tjoelker *et al.* (1999*b*)
Betula papyrifera	shoot	2.19	2.27	Growth temperature 24 / 18°C	Tjoelker *et al.* (1999*b*)
Betula papyrifera	shoot	2.03	1.85	Growth temperature 30 / 24°C	Tjoelker *et al.* (1999*b*)
Larix laricina	shoot	2.04	2.22	Growth temperature 18 / 12°C	Tjoelker *et al.* (1999*b*)
Larix laricina	shoot	1.95	1.87	Growth temperature 24 / 18°C	Tjoelker *et al.* (1999*b*)
Larix laricina	shoot	2.03	2.15	Growth temperature 30 / 24°C	Tjoelker *et al.* (1999*b*)
Picea mariana	shoot	2.18	2.26	Growth temperature 18 / 12°C	Tjoelker *et al.* (1999*b*)
Picea mariana	shoot	2.05	1.97	Growth temperature 24 / 18°C	Tjoelker *et al.* (1999*b*)
Picea mariana	shoot	2.00	1.99	Growth temperature 30 / 24°C	Tjoelker *et al.* (1999*b*)
Pinus banksiana	shoot	2.02	2.08	Growth temperature 18 / 12°C	Tjoelker *et al.* (1999*b*)
Pinus banksiana	shoot	2.06	2.09	Growth temperature 24 / 18°C	Tjoelker *et al.* (1999*b*)
Pinus banksiana	shoot	2.01	2.11	Growth temperature 30 / 24°C	Tjoelker *et al.* (1999*b*)
Liquidambar styraciflua	leaf	2.15	1.96		Hamilton *et al.* (2001)
Pinus taeda	leaf	2.79	2.62		Hamilton *et al.* (2001)
Scirpus olney	stem	1.85	2.25		Azcón-Bieto *et al.* (1994)
Lindera benzoin	leaf	1.71	1.51		Azcón-Bieto *et al.* (1994)
Spartina patens	leaf	3.27	2.04		Azcón-Bieto *et al.* (1994)
Populus alba	stem	3.36	2.46	Plot 1	Gielen *et al.* (2003)
Populus alba	stem	3.50	3.94	Plot 2	Gielen *et al.* (2003)
Populus alba	stem	5.89	2.80	Plot 3	Gielen *et al.* (2003)
Populus nigra	stem	1.78	2.48	Plot 1	Gielen *et al.* (2003)
Populus nigra	stem	3.41	1.69	Plot 2	Gielen *et al.* (2003)
Populus nigra	stem	1.91	5.23	Plot 3	Gielen *et al.* (2003)
Populus euramericana	stem	1.95	1.91	Plot 1	Gielen *et al.* (2003)
Populus euramericana	stem	1.28	1.64	Plot 2	Gielen *et al.* (2003)
Populus euramericana	stem	2.51	7.62	Plot 3	Gielen *et al.* (2003)
Pinus sylvestris	needle	2.44	2.50	current year	Zha *et al.* (2002)
Pinus sylvestris	needle	2.08	2.14	1-year old	Zha *et al.* (2002)
Pinus sylvestris	needle	1.83	1.94	2-year old	Zha *et al.* (2002)
Liquidambar styraciflua	stem	2.10	1.70	Growing season	Edwards *et al.* (2002)
Liquidambar styraciflua	stem	1.90	2.20	Dorman season	Edwards *et al.* (2002)
Picea abies	stem	1.95	1.96	Spring	Janouš *et al.* (2000)
Picea abies	stem	2.15	2.15	Summer	Janouš *et al.* (2000)
Picea abies	stem	2.09	2.09	Autumn	Janouš *et al.* (2000)
Picea abies	branch	2.43	2.90	Spring	Janouš *et al.* (2000)
Picea abies	branch	2.52	2.94	Summer	Janouš *et al.* (2000)
Picea abies	branch	2.15	2.45	Autumn	Janouš *et al.* (2000)
Picea abies	root	2.51	2.43	Spring	Janouš *et al.* (2000)
Picea abies	root	2.55	2.51	Summer	Janouš *et al.* (2000)
Picea abies	root	2.52	2.29	Autumn	Janouš *et al.* (2000)
Pinus ponderosa	stem	1.67	2.20		Carey *et al.* (1996)
Leaf / shoot / branch average ± SE		2.12 ± 0.06	2.19 ± 0.07		
Stem average ± SE		2.46 ± 0.15	2.72 ± 0.22		
Root average ± SE		2.53 ± 0.12	2.41 ± 0.06		
Overall average ± SE		2.24 ± 0.09	2.37 ± 0.13		

suggest that longer-term adjustments in leaf structure under low soil water availability may result in increased *R* but a lower temperature-sensitivity (Q_{10}) of dark *R*.

Irradiance

There is growing evidence that the Q_{10} of leaf respiratory CO_2 release is often lower in light than in darkness, regardless of growth temperature (Table 2; Fig. 3). Although Q_{10} values in the light and dark are highly variable, a majority of studies have found that Q_{10} values in the light ($Q_{10\,/\,light}$) are lower than those in darkness ($Q_{10\,/\,dark}$) (e.g. 10 of the 15 comparisons shown in Table 2). In some cases, $Q_{10\,/\,light}$ is close to 1 [i.e. temperature insensitive; e.g. *Gossypium hirsutum* (Harley *et al*. 1992); *Zea mays* (Loreto *et al*. 2001); *Fagus sylvatica* (Bruhn 2002); *Eperua grandiflora* (Pons and Welschen 2003)], while no differences in $Q_{10\,/\,light}$ and $Q_{10\,/\,dark}$ values were found in three species [*Spinacia oleracea* (Brooks and Farquhar 1985), *Heteromeles arbutifolia* and *Lepechinia fragans* (Villar *et al*. 1995)]. Shapiro *et al*. (2004) also reported that $Q_{10\,/\,light}$ and $Q_{10\,/\,dark}$ values were similar in *Xanthium strumarium* experiencing several growth treatments (with the exception

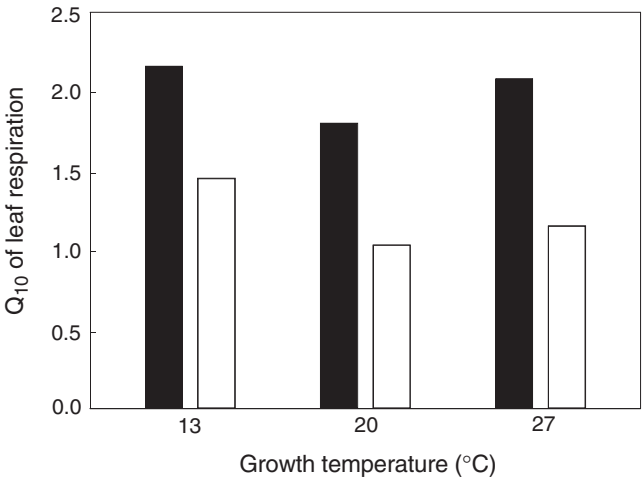

Fig. 3. The effect of irradiance and growth temperature on the Q_{10} (between 6 and 27°C) of *Plantago major* leaf respiration (OK Atkin, I Sheurwater, TL Pons unpublished data). *R* in the light (open bars) was measured using the Laisk (1977) method, as described in Atkin *et al*. (2000*c*). Closed bars, dark. Q_{10} values were calculated through fitting first order linear regressions to log R (using average rates of R) *v.* measuring temperature; thus, only a single Q_{10} value was obtained for each growth temperature / irradiance combination.

Table 2. Values of Q_{10} of respiration in leaves in the light and darkness

Values of Q_{10} were obtained from the published sources shown or derived from temperature-response functions of respiration and / or from table values of both temperature and respiration rates. Methods for determination of leaf respiration in light differ between studies and are either indicated or the primary reference given

Species	Method	$Q_{10\,/\,dark}$	$Q_{10\,/\,light}$	Measurement temperature range	Comments	Reference
Eperua grandiflora	Laisk (1977)	2.5	1	28–38°C		Pons and Welschen (2003)
Eucalyptus pauciflora	Laisk (1977)	2.21	1.61	6–25°C		Atkin *et al*. (2000*b*)
Fagus sylvatica	Laisk (1977)	2.36	1.2	15–25°C		Bruhn (2002)
Gossypium hirsutum	Farquhar *et al*. (1980)	3.19	1	18–35°C		Harley *et al*. (1992)
Heteromeles arbutifolia	Laisk (1977)	2.33	2.04	10–30°C		Villar *et al*. (1995)
Lepechinia fragans	Laisk (1977)	2.37	4.74	10–30°C		Villar *et al*. (1995)
Plantago major	Laisk (1977)	2.16	1.45	13–27°C	Growth temperature: 13°C	OK Atkin unpublished data
Plantago major	Laisk (1977)	1.79	0.91	13–27°C	Growth temperature: 20°C	OK Atkin unpublished data
Plantago major	Laisk (1977)	2.08	1.15	13–27°C	Growth temperature: 27°C	OK Atkin unpublished data
Rumex acetosa	Keeping ambient $[CO_2]$ at 5 ppm	2.3	1.8	15–30°C		Holmgren and Jarvis (1967)
Xanthium strumarium	Kok (1948)	3.37	3.33	23–33°C	High growth $[CO_2]$, high N	Shapiro *et al*. (2004)
Xanthium strumarium	Kok (1948)	2.00	2.01	23–33°C	Ambient growth $[CO_2]$, high N	Shapiro *et al*. (2004)
Xanthium strumarium	Kok (1948)	3.00	4.91	23–33°C	High growth $[CO_2]$, low N	Shapiro *et al*. (2004)
Xanthium strumarium	Kok (1948)	1.94	1.89	23–33°C	Ambient growth $[CO_2]$, low N	Shapiro *et al*. (2004)
Zea mays	$^{12}CO_2$ efflux into $^{13}CO_2$ atmosphere	1.78	1	25–42°C	Lower range of the two temperature ranges reported	Loreto *et al*. (2001)

of plants grown under elevated CO_2 and low N, where $Q_{10\,/\,light}$ was greater than $Q_{10\,/\,dark}$). Thus, while light often reduces the Q_{10} of *R*, not all species exhibit lower Q_{10} values in the light.

Underpinning the effect of irradiance on the Q_{10} (where it occurs) is the inhibitory effect of light on respiratory CO_2 release per se, particularly at high measuring temperatures. All of the above studies have applied the Kok (1948) and Laisk (1977) methods, except from Loreto *et al*. (1999, 2001) who made use of a new technique based on the insensitivity to ^{13}C by an infrared gas analyser. This inhibitory effect by light has been confirmed by other techniques as well, including a ^{14}C-labelling technique that takes into account refixation of respiratory CO_2 by Rubisco (Pärnik and Keerberg 1995; McCashin *et al*. 1988). In contrast, using the ^{14}C method, Hurry *et al*. (1996) found that light stimulated *R* in winter rye by 31%, showing that light does not necessarily inhibit *R* in all species.

Leaf position within a canopy

Recent studies have shown that there is considerable within-canopy variability in the Q_{10} of leaf *R* in some trees (Bolstad *et al*. 1999; Griffin *et al*. 2002; Turnbull *et al*. 2003). In some studies, leaves in the lower part of the canopy exhibit higher Q_{10} values than leaves in the upper canopy (Griffin *et al*. 2002; Turnbull *et al*. 2003). As a result, scaling leaf respiratory CO_2 loss to the whole canopy level tends to underestimate CO_2 loss if the assumptions are based on the Q_{10} values of lower canopy leaves alone (Turnbull *et al*. 2003). In contrast, in a survey of 18 broad-leaved forest tree species in the southern Appalachians of North America, Bolstad *et al*. (1999) found no consistent trend of Q_{10} values with respect to canopy position. Further work is needed to assess the extent to which upper and lower canopy leaves differ systematically in their Q_{10} values and how it may be linked to photosynthesis.

Leaves v. *roots*

A survey of the literature shows that Q_{10} values (typically within the 10–30°C measurement temperature range) range from 1.4 to 4.2 for leaf *R* (Azcón-Bieto 1992; Larigauderie and Körner 1995; Tjoelker *et al*. 2001) and 1.1 to 4.6 for root *R* (Higgins and Spomer 1976; Boone *et al*. 1998; Tjoelker *et al*. 1999*b*). This suggests that there is little difference in overall range of Q_{10} values exhibited by leaves and roots. However, when Loveys *et al*. (2003) compared 16 species under the same growth conditions (hydroponics in growth cabinets) they found that the mean Q_{10} values exhibited by mature leaves (2.03–2.39) were generally higher than those of whole root systems or root segments (1.58–1.61) when determined over the 15–25°C measurement temperature range. This general response may suggest that the ability of leaves to more readily access recently fixed carbon increases the temperature response of leaf *R* compared with that of root *R*.

One factor that needs to be considered when comparing published leaf and root Q_{10} values is the nature of the tissue used in different studies. In most studies, rates of leaf *R* are measured using fully expanded individual leaves. In contrast, measurements of *R* in roots are made using whole root systems (e.g. Smakman and Hofstra 1982; Bouma *et al*. 1997; Covey-Crump *et al*. 2002; Loveys *et al*. 2003) or root segments of differing age or function (e.g. Higgins and Spomer 1976; Crawford and Palin 1981; Sowell and Spomer 1986; Weger and Guy 1991; Zogg *et al*. 1996; Pregitzer *et al*. 1997, 1998; Burton *et al*. 2002; Comas and Eissenstat 2004). Recent studies with leaves have shown that the Q_{10} of mature fully expanded leaves is higher than that of immature leaves (A Armstrong, OK Atkin unpublished data). In contrast, Zha *et al*. (2001) reported that maintenance respiration of fully expanded Scots pine needles was more sensitive to increases in growth temperature than growth respiration in expanding needles. Q_{10} values of 1.5 for coarse woody roots and 2.0 for fine roots (<2 mm diameter) were reported in a *Pinus radiata* stand (Ryan *et al*. 1996). Thus, although there is variability in the temperature response of young *v.* old tissues, estimates of Q_{10} in whole root or shoot systems can clearly depend on the proportion of the root or shoot system represented by immature and mature roots or leaves and the Q_{10} of each developmental stage.

Seasonal variation

Under field conditions, the Q_{10} of leaf *R* is higher in winter and autumn than in summer in evergreen species [*Chamaecyparis obtusa* (Paembonan *et al*. 1991); *Picea abies* (Stockfors and Linder 1998); *Eucalyptus pauciflora* (Atkin *et al*. 2000*b*); *Pinus sylvestris* (Zha *et al*. 2003, 2005) and *Pinus banksiana* (MG Tjoelker, J Oleksyn, PB Reich unpublished data)], even when compared at the same measurement temperatures. However, *Eucalyptus pauciflora* showed little seasonal variation in Q_{10} over much of the year (Atkin *et al*. 2000*b*). Q_{10} values were only greater on days when daily average and minimum air temperatures were below 6°C and –1°C, respectively. Also, Q_{10} of branch *R* in a *Fagus sylvatica* stand was found to be relatively constant (around 1.7) throughout the course of the year (Damesin *et al*. 2002). Zha *et al*. (2004) found that Q_{10} values of stem respiration were highest in the growing season.

Growth temperature

Several studies have shown that changing growth temperature also affects the Q_{10} of leaf and root *R* (e.g. schematically shown in Fig. 1; Wager 1941; Atkin *et al*. 2000*b*; Covey-Crump *et al*. 2002; Zha *et al*. 2002; Loveys *et al*. 2003). Differences in Q_{10} (for a common measurement temperature interval) between plants grown at contrasting growth temperatures ultimately arises from changes in the shape of the short-term temperature-response function. In some cases, a growth temperature-dependent change in the Q_{10}

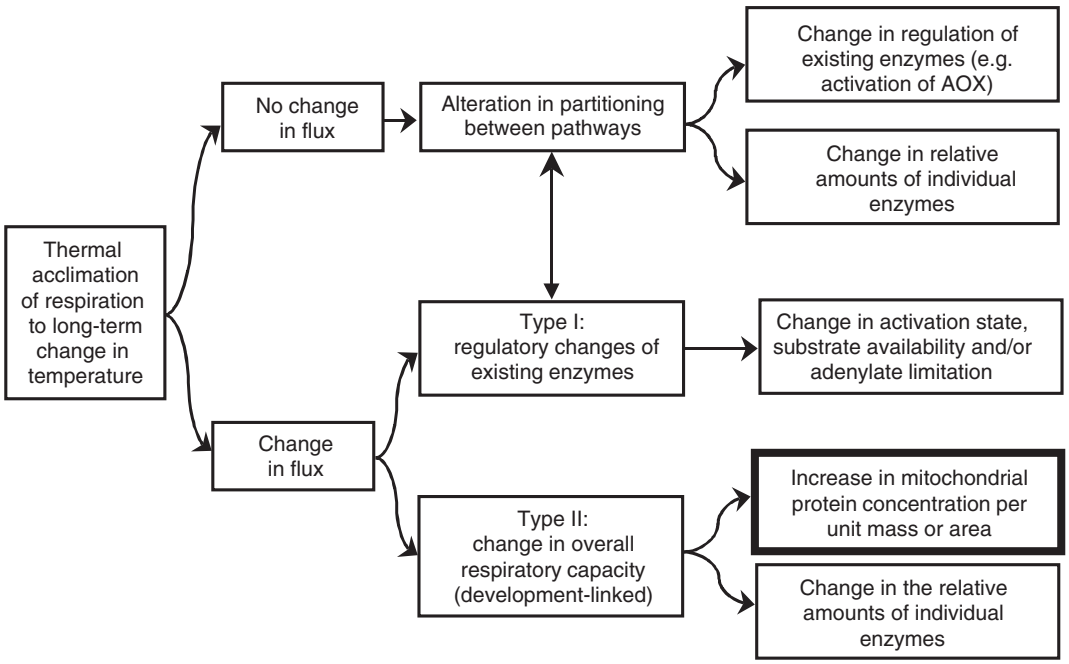

Fig. 4. Schematic presentation of the types of acclimation exhibited by plant respiration. 'Coarse control' is depicted by the heavy border surrounding Type II acclimation mechanisms (i.e. increase in mitochondrial protein content). All other mechanistic examples represent 'fine control' of acclimation (i.e. no change in flux, Type I acclimation and Type II acclimation through changes in relative amounts of individual enzymes). AOX, alternative oxidase.

reflects changes in the availability of respiratory substrate and / or degree of adenylate restriction of *R* (Fig. 4; Atkin and Tjoelker 2003). Support for this suggestion comes from the fact that exposure to elevated atmospheric CO_2 (which increases photosynthesis and steady-state carbohydrate concentrations) also increases the Q_{10} of leaf or needle *R* (Zha *et al*. 2002; Shapiro *et al*. 2004).

Growth-temperature effects on Q_{10} also appear to differ between plants exposed to a new thermal regime for several days and leaves and roots that develop under contrasting temperatures. Covey-Crump *et al*. (2002) found that the Q_{10} (between 15–23°C) of *Plantago lanceolata* root *R* was greater at low measurement temperatures in plants exposed to 15°C for 7 d than in plants kept at 23°C. Similarly, Rook (1969) found that the Q_{10} (between 15–30°C) of leaf *R* in *Pinus radiata* seedlings grown at 33 / 28°C increased following a 2-d exposure to 15 / 10°C (rates of *R* measured at 15–30°C increased significantly, whereas there was no change in *R* measured at 8°C). Conversely, shifting of 15 / 10°C grown plants to 33 / 28°C resulted in the Q_{10} decreasing within 2 d (again, no change in *R* at 8°C was observed). However, in another study shifting from a growth temperature of 25 / 20°C to 15 / 10°C for 7 d had no effect on the Q_{10} of root *R* of several species (calculated using rates of *R* measured at 15 and 25°C; Loveys *et al*. 2003). Moreover, no growth-temperature-dependent differences in Q_{10} values were apparent in plant leaves or roots that had developed at different temperatures (i.e. were not shifted; Tjoelker *et al*. 1999*b*; Loveys *et al*. 2003). Thus, the effect of growth temperature on the Q_{10} of *R* (and, thus, the degree of acclimation) is variable, being dependent on species and on the range of growth temperatures being compared.

Inter-biome variation

To successfully predict annual CO_2 release in contrasting biomes, the extent to which Q_{10} values differ between biomes may be an important issue in modelling. When Q_{10} values are determined at measurement temperatures experienced by plants in the field, plants growing in cold climates exhibit higher Q_{10} values than their warm-climate counterparts [e.g. Tjoelker *et al*. (2001) found that the mean Q_{10} values of arctic and tropical plants were 2.56 and 2.14, respectively]. Because of this, short-term changes in temperature can have a greater effect on respiratory flux in plants growing in the arctic than in plants grown in tropical regions.

To what extent are the inter-biome differences in Q_{10} a reflection of inherent differences between plant species characteristic of the contrasting biomes? To assess this question, comparisons of Q_{10} values need to be made over a common measurement temperature range (owing to temperature dependence of the Q_{10}; see Tjoelker *et al*. 2001 and Atkin and Tjoelker 2003). Criddle *et al*. (1994) found that temperature-corrected Q_{10} values varied with climate of origin amongst woody species, but not amongst annuals or

herbaceous perennials. However, in a controlled-environment experiment, Larigauderie and Körner (1995) found no evidence that temperature-corrected leaf Q_{10} values depend on altitude of plant origin. There was no systematic variation in leaf or root Q_{10} values amongst species characteristic of alpine, temperate and arid environments in the study by Loveys *et al*. (2003). When Tjoelker *et al*. (2001) compared Q_{10} values of plants in arctic, boreal, and temperate biomes over a common temperature range, they found that the mean Q_{10} values were relatively similar (2.42 for arctic, 2.22 for boreal, an 2.31 for temperate biomes), compared with when Q_{10} values were measured over the temperatures experienced by plants in the field. Moreover, Burton *et al*. (2002) found that the Q_{10} of fine root respiration of forest trees was similar in North American biomes when compared at a common temperature (Table 3). Thus, even though some differences in Q_{10} occur amongst biomes when compared at low and high measurement temperatures (Tjoelker *et al*. 2001; Table 4), overall the large inter-biome differences in Q_{10} are likely the result of differences in measuring temperature in the thermally contrasting biomes. Thus, differences in Q_{10} values amongst biomes are unlikely to reflect inherent differences in the temperature sensitivity of *R* for species characteristic of each biome (i.e. there has been no adaptive change in the Q_{10} of *R*).

Further support for the suggestion that Q_{10} values do not differ systematically among contrasting plant species comes from the fact that most species exhibit Q_{10} values that fall within a narrow range when values are compared at a common measurement temperature interval. For example, Ivanova *et al*. (1989) found that the mean Q_{10} for leaf *R* in 34 temperate and Arctic plant species was 2.45 (between 10 and 20°C measurement temperature range) with the upper and lower 95% confidence intervals being 2.62 and 2.27, respectively. Similarly, the mean leaf Q_{10} of 59 species (15°C midpoint) reported by Tjoelker *et al*. (2001) was 2.50, with the upper and lower 95% confidence intervals of 2.62 and 2.39, respectively. In a review of published values of 125 species, Larigauderie and Körner (1995) found that the majority of species exhibited leaf Q_{10} values between 2.0 and 2.5, with the overall mean being 2.3. Thus, despite large differences between the highest and lowest Q_{10}, contrasting species often exhibit relatively similar Q_{10} values over a given measurement temperature range.

Acclimation: characteristics, variability, mechanisms and consequences for *R* / *P*

As stated earlier, most GCMs assume that the changes in the long-term growth temperature will not alter rates of *R* at a common measurement temperature (i.e. *R* does not

Table 3. Q_{10} values for fine root respiration of forest tree species of North American biomes

Data were obtained from Burton *et al*. (2002). MAT, mean annual temperature; LTER, long-term ecological research site (USA National Science Foundation)

Biome	Location	Species / stand and type	MAT[2] (°C)	Q_{10} (6–24°C)
Boreal	Bonanza Creek LTER, Alaska, USA	*Populus balsamifera*	–3.3	2.4
		Picea glauca		2.9
Cold-temperate	Michigan, USA	*Acer saccharum*	3.8	2.7
		Pinus resinosa plantation		3.0
Montane cool-temperate	Coweeta LTER, North Carolina, USA	Mixed hardwoods	9.4	2.4
		Quercus–Carya	11.1	3.1
		Liriodendron tulipifera	12.7	2.6
Semi-arid	Sevilleta LTER, New Mexico, USA	*Pinus edulis*	12.7	2.6
		Juniperus monosperma	12.7	2.4
Warm-temperate	Georgia, USA	Mixed *Quercus*	16.5	2.4
	Florida, USA	*Pinus elliottii* plantation	20.0	2.5

Table 4. Mean Q_{10} of leaf dark respiration for plant species of various biomes measured in their growth environments at a range of measurement temperatures

(Adapted from Ivanova *et al*. 1989). *n*, number of species sampled

Biome	Location	*n*	Measurement temperature interval (°C) 5–15	10–20	15–25	20–30	25–35	30–40	35–45	45–55
Arctic	Wrangel Island	18	2.95	2.42	2.13	1.94	1.58	–	–	–
Sub-arctic	Hibbins Mts	17	–	1.86	1.96	1.92	1.73	1.58	1.39	–
Boreal	St Petersberg	18	–	2.48	2.05	1.95	–	1.71	1.46	–
Temperate	Caucasus	19	–	–	2.44	2.17	1.91	1.77	–	–
Desert	Karakum	14	–	–	–	1.80	–	1.84	2.18	2.05

acclimate). Rather, most simulation models assume that *R* responds to short- and long-term changes in temperature in a fixed, exponential manner ($Q_{10} = 2.0$). This might not be a problem if plant *R* did not acclimate to long-term changes in temperature. However, plant *R* often does acclimate. Here, we outline the characteristics of acclimation and the extent to which acclimation varies among and within plant species.

Overview

An example of thermal acclimation is shown in Fig. 1, where exposure of a warm-grown plant to the cold for several days results in an increase in the rate of *R* at a common measurement temperature (Rook 1969; Chabot and Billings 1972; Pisek *et al*. 1973; Larigauderie and Körner 1995; Körner 1999; Atkin *et al*. 2000*b*; Covey-Crump *et al*. 2002; Zha *et al*. 2002, 2005; Bolstad *et al*. 2003). Conversely, exposure to high temperatures results in a decrease in the rate of *R* at a common temperature (Fig. 1). Differences in the rate of *R* at standard measurement temperatures are also commonly exhibited by plants that grew and developed under contrasting temperature regimes (either in the laboratory or in the field) (e.g. Figs 1, 3; Billings and Mooney 1968; Chabot and Billings 1972; Körner and Larcher 1988; Collier and Cummins 1990; Semikhatova *et al*. 1992; Collier 1996; Goldstein *et al*. 1996; Arnone and Körner 1997; Zha *et al*. 2002). In some cases, acclimation is associated with a change in the rate of *R* primarily at moderate to high measuring temperatures, with little or no change in *R* at low measuring temperatures (i.e. the short-term Q_{10} value changes) (Fig. 1; see below). Atkin and Tjoelker (2003) defined this as 'Type I acclimation'; it appears to reflect a change in the availability of respiratory substrate and / or degree of adenylate restriction of *R* (Fig. 4). Type I acclimation *R* can occur within a 1–2-d period following a change in ambient temperature (Rook 1969; Billings *et al*. 1971; Chabot and Billings 1972; Atkin *et al*. 2000*b*; Covey-Crump *et al*. 2002; Bolstad *et al*. 2003), raising the possibility that plant *R* may dynamically acclimate to changes in thermal environment with an onset of the acclimation processes within perhaps hours. Changes in gene expression may also occur, but are not essential for the overall change in respiratory flux (Fig. 4). In other cases, acclimation is associated with an increase in the rate of *R* over a wide range of measurement temperatures ('Type II acclimation'; Fig. 1). Type II acclimation is likely associated with temperature-mediated changes in respiratory capacity that can be maximally realised through growth of new tissues with altered morphology and biochemistry (Fig. 4; Atkin and Tjoelker 2003). Total respiratory capacity might be altered as a result of changes in the density of mitochondria (Miroslavov and Kravkina 1991) and / or amount of total protein invested in the respiratory chain (Klikoff 1966, 1968). Type II acclimation could be associated with changes in the relative amounts of particular enzymes (e.g. AOX *v.* complex IV; Ribas-Carbó *et al*. 2000). Intermediate cases of acclimation (i.e. between Types I and II) are likely, particularly in individual plants that experience long-term changes in temperature depending on the extent to which respiratory capacity is altered in pre-existing and newly formed leaves and roots. Another characteristic of acclimation (particularly Type II acclimation) is that it can result in respiratory homeostasis [i.e. identical rates of *R* in plants grown and measured in contrasting temperatures (Körner and Larcher 1988; Semikhatova *et al*. 1992; Goldstein *et al*. 1996; Arnone and Körner 1997; Körner 1999; Atkin *et al*. 2000*b*)] (Fig. 1). A good example comes from the work of Xiong *et al*. (2000), who showed that two Antarctic species, *Colobanthus quitensis* and *Deschampsia antarctica*, are capable of maintaining constant rates of *R* (measured at their respective daytime growth temperature) when grown at three different temperatures. Such changes can result in annual respiratory CO_2 release being substantially reduced in leaves and roots that exhibit a high degree of thermal acclimation of *R* compared with that of tissues that do not acclimate (Fig. 2; Atkin *et al*. 2000*a*).

Variation in the degree of acclimation

Inter-specific variation

There is growing evidence that the degree of respiratory acclimation in leaves and roots varies substantially, both within and amongst individual species (Larigauderie and Körner 1995; Tjoelker *et al*. 1999*a*; Loveys *et al*. 2003). For example, Frantz *et al*. (2004) reported no acclimation of whole-plant respiration in young, rapidly growing plant communities experiencing contrasting night temperatures for a 20-d period. Moreover, Larigauderie and Körner (1995) found that growth at low temperatures resulted in little or no acclimation of leaf *R* in several alpine (*Poa alpina*, *Leucanthemopsis alpina*, *Luzula alpino-pilosa*, *Carex foetida*, *Cirsium alpinum* and *Saxifraga biflora*) and lowland (*Luzula campestris*, *Carex caryophyllea* and *Cirsium acaule*) species. In contrast, acclimation of leaf *R* occurred in *Ranunculus acris*, *Anthoxanthum odoratum*, *Leucanthemum alpinum*, *Poa pratensis*, *Taraxacum alpinum*, *T. officinale* (Larigauderie and Körner 1995) and *Ranunculus glacialis* (Arnone and Körner 1997).

Are there systematic differences amongst plant taxa in the degree to which leaf *R* acclimates? Tjoelker *et al*. (1999*a*) found that broad-leaved tree species exhibited a lower degree of acclimation of leaf *R* than selected conifer species, suggesting that acclimation might be predicted using structural and / or functional traits. Differences in ability to acclimate were also observed amongst six of the eight genera used by Larigauderie and Körner (1995). For example, the two *Taraxacum* species exhibited a greater degree of acclimation than did the two *Cirsium*

species. However, Larigauderie and Körner (1995) found no evidence that within a given genus, alpine and lowland plant species differ in their extent of leaf *R* acclimation to contrasting growth temperatures. In contrast, Loveys *et al*. (2003) showed that slow-growing species exhibited a higher degree of leaf *R* acclimation than their fast-growing counterparts in four of six genera. The degree of acclimation was not, however, related to inherent differences in whole plant maximum RGR when all 16 species were considered (Loveys *et al*. 2003). Thus, while there is some evidence that the degree of acclimation differs systematically amongst taxa in some studies, there are also many results that contradict this.

The degree of thermal acclimation of root *R* is also highly variable. Acclimation of root respiration occurs in *Plantago lanceolata* (Smakman and Hofstra 1982; Loveys *et al*. 2002, 2003), *Zostera marina* (Zimmerman *et al*. 1989), *Citrus volkameriana* (Bryla *et al*. 1997, 2001), *Festuca ovina*, *Juncus squarrosus*, *Nardus stricta* (Fitter *et al*. 1998), *Bellis perennis*, *Poa annua* (Gunn and Farrar 1999) and *Holcus lanatus* (Edwards *et al*. 2004). In contrast, there is little or no acclimation of root *R* in field-grown *Acer saccharum* and *Pinus resinosa* to seasonal changes in temperature (Burton and Pregitzer 2003). Moreover, there was no obvious acclimation in roots of two *Picea* species (Sowell and Spomer 1986; Weger and Guy 1991) and *Abies lasiocarpa* (Sowell and Spomer 1986). Similarly, while acclimation to changes in growth temperature results in near-perfect homeostasis of *R* in *Citrus volkameriana* in wet soils, no acclimation occurs in roots of the same species growing in dry soils (Bryla *et al*. 1997). Even in species where root *R* does acclimate, the degree of acclimation is variable. For example, in a comparison of root *R* of five cold-grown (18 / 12°C) and warm-grown (30 / 24°C) boreal tree species at a set measuring temperature (18°C), warm-grown plants exhibited root *R* rates that were 50–74% of that exhibited by the cold-grown plants (Tjoelker *et al*. 1999*a*). Similarly, the degree of acclimation of root *R* was highly variable amongst 16 species in the study by Loveys *et al*. (2003).

Nitrogen-dependent variation

Low N availability does not appear to influence the degree of respiratory temperature acclimation exhibited by plants transferred from one growth temperature to another for several days. Atkinson and Atkin (LJ Atkinson, OK Atkin unpublished data) grew several herbaceous plant species at 25 / 20°C, at both high and low N availability (2000 and 25 μM, respectively); these plants were then shifted to 15 / 10°C for 7 d, and the degree of acclimation of root *R* was determined using methods described by Loveys *et al*. (2003). Although homeostasis was not observed in any of the species, plants grown at high and low N availability exhibited significant and similar degrees of temperature acclimation of root *R*. Low N supply did, however, result in a slower specific rate of *R* in all species; consequently, the absolute change in *R* following extended exposure to low temperature was lower in the low-N plants.

Variations that are development-dependent

There is evidence that the degree of temperature acclimation of *R* is lower in pre-existing plant tissues shifted from one temperature to another (an example of 'Type I' acclimation; Fig. 1) than in leaves and roots that develop at the growth temperature ('Type II' acclimation) (Atkin and Tjoelker 2003). In a comparison of nine species, Loveys *et al*. (2003) found that the degree of respiratory acclimation was greater in leaves and roots that had developed under contrasting temperatures (18, 23 and 28°C) than in 25°C-grown plants shifted to 15°C for 7 d (Fig. 5). Moreover, acclimation of *R* to 5°C was substantially greater in *Arabidopsis thaliana* leaves that developed at 5°C than that of warm-grown leaves shifted to 5°C for several days (Talts *et al*. 2004). A similar requirement for the development of new tissues has been reported for thermal acclimation of *P*; studies with winter rye and *Arabidopsis* have shown that for full acclimation of *P* to a low growth temperature, new leaves need to be formed in the cold (Hurry *et al*. 1995; Strand *et al*. 1997, 2003). Cold-developed leaves are thicker, more dense, exhibit higher nitrogen concentrations and have higher transcript and activity levels of photosynthetic and sucrose synthesis enzymes than their warm-grown counterparts (Stitt and Hurry 2002).

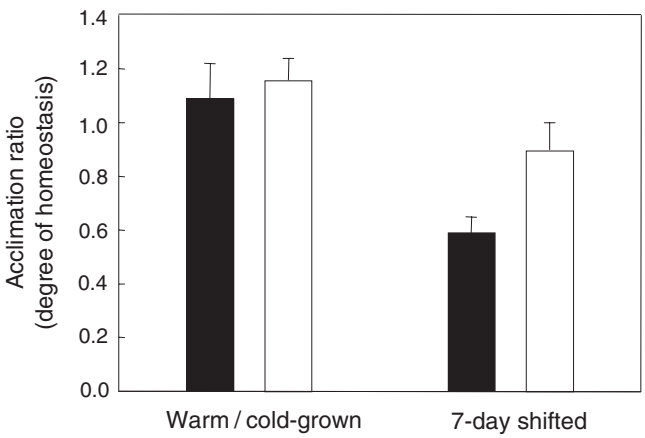

Fig. 5. Average acclimation ratios (see Loveys *et al*. 2003 for a description of how acclimation ratio was calculated) of 9–16 plant species. High ratios indicate a high degree of acclimation. The warm / cold grown ratios represent comparisons of 16 species where leaves (closed bars) and roots (open bars) develop under contrasting temperatures. In the 7-d shift comparison, nine species were shifted from 25 to 15°C for 7 d and the degree of acclimation assessed. Independent *t*-tests revealed that there was no significant difference between leaves and roots in the warm / cold grown ratios (16 species), while there was a significant difference between leaves and roots in the 7-d shift comparison ($P < 0.01$).

There are two other areas where stage of development needs to be considered when dealing with acclimation of plant *R* to temperature. First, the effect of growth temperature on rates of *R* at a set temperature may depend on the age of plant leaves or roots. Recently, Armstrong and Atkin (A Armstrong, OK Atkin unpublished data) found that immature leaves of *A. thaliana* exhibited near-identical rates of *R* at any given temperature (no acclimation), regardless of whether the tissue developed under 25 or 5°C. In contrast in mature leaves, rates of leaf *R* at any given temperature were faster in cold-acclimated than warm-acclimated leaves (see above). These findings suggest that although thermal environment during development likely leads to long-term effects on *R* response to temperature (i.e. acclimation), the full extent of the acclimation response is only evident in fully developed leaves or roots. Second, the question of whether roots and leaves of the same plant differ in their ability to acclimate *R* to contrasting temperatures also depends on development. For example, Loveys *et al*. (2003) found no evidence that leaves and roots differ in their magnitude of acclimation when both tissues develop at the prevailing growth temperature (Fig. 5). Similarly, Tjoelker *et al*. (1999*a*) also reported no systematic difference in the degree of acclimation of roots and leaves in tree seedlings that develop under contrasting temperatures. However, Loveys *et al*. (2003) found that roots exhibited a higher degree of acclimation than leaves when plants were shifted from 25 to 15°C for 7 d. As Loveys *et al*. (2003) measured whole root systems (i.e. young and old roots), development of new roots at the new growth temperature could account for a gradual acclimation of the whole root system.

Component of the daily temperature regime to which R *acclimates*

Thermal acclimation of *R* has to be taken into account when modelling responses of *R* to a warmer climate. The most straightforward approach may be to assume that *R* acclimates to the daily mean temperature, and then use forecasted daily mean temperatures to model, e.g. an annual release of CO_2 for a specific type of species or vegetation. So far, only a few studies have addressed the question of which component of the daily temperature regime *R* acclimates to. For the sake of simplicity, the diurnal fluctuations in temperature can be divided into a daily minimum, mean, and maximum temperature. The general conclusion is that *R* does not acclimate to the daily mean temperature in all species and / or tissues (Fitter *et al*. 1998; Atkin *et al*. 2000*b*). Will (2000) and Covey-Crump *et al*. (2002) examined the response of *R* in *Pinus taeda* leaves and *Plantago lanceolata* roots, respectively. Niether found that respiration acclimates to the daily average temperature. Covey-Crump *et al*. (2002) concluded that root respiration acclimates to the night-time minimum temperature, a conclusion that is supported in part by work on field grown *Eucalyptus pauciflora* leaves in south-eastern Australia (Atkin *et al*. 2000*b*). However, night temperature was not the dominant factor in the study by Will (2000). Moreover, in a study by Bruhn (2002) assessing whether generalisations could be made among and / or within 10 contrasting genotypes, the temperature regime that *R* acclimated to was highly variable after transfer to different thermal environments. Thus, while there is some evidence that nighttime temperatures may be of particular importance, the results of Will (2000) and Bruhn (2002) suggest that generalisations are not yet possible.

Mechanisms responsible for variability in acclimation

What factors are responsible for the variability in degrees of acclimation? Given the link between developmental plasticity and cold acclimation and respiration (see previous section), it seems likely that interspecific differences in Type II acclimation may reflect differences in the plasticity of contrasting species when challenged with a new growth temperature. This leads to the prediction that plant species that produce long-lived leaves and roots and that are relatively slow at generating new tissues may exhibit a relatively limited ability to acclimate at the whole-plant level to long-term changes in temperature (Atkin and Tjoelker 2003). In species that are highly plastic, Type II acclimation is likely associated with changes in glycolytic and / or mitochondrial proteins when new leaves develop following a change in growth temperature. What is less obvious, however, are the molecular and biochemical events that lead to the developmentally linked changes in *R*. Some factors that may contribute are the extent to which acclimation is (1) a response to temperature-dependent changes in substrate availability (Fig. 6*A*), (2) a result of the maintenance of homeostatic levels of ATP synthesis across a range of contrasting growth temperatures (to support growth, maintenance and / or ion exchange processes) (Fig. 6*B*) and / or (3) a reduction in the production of reactive oxygen species (ROS; through avoiding accumulation of excess redox equivalents) (Fig. 6*C*). Reactive oxygen species are produced by aerobic metabolism in chloroplasts and mitochondria and can damage proteins, lipids and DNA (Møller 2001). Here, we deal with each of these possibilities.

(1) *Responding to substrate availability*. Changes in growth temperature often result in a change in the concentration of soluble sugars and thus availability of substrates to the respiratory system (Mooney and Billings 1965; Warren Wilson 1966; Farrar and Williams 1991; Hurry *et al*. 1994; Atkin *et al*. 2000*b*; Oleksyn *et al*. 2000; Covey Crump *et al*. 2002). Why is this? Although changes in growth temperature can affect the rate of CO_2 fixation and resultant sucrose synthesis, growth temperature often has a greater relative affect on the rate of substrate use (by growth and maintenance processes, as well as respiration *per se*) and translocation (Körner 1999). As a result, the balance

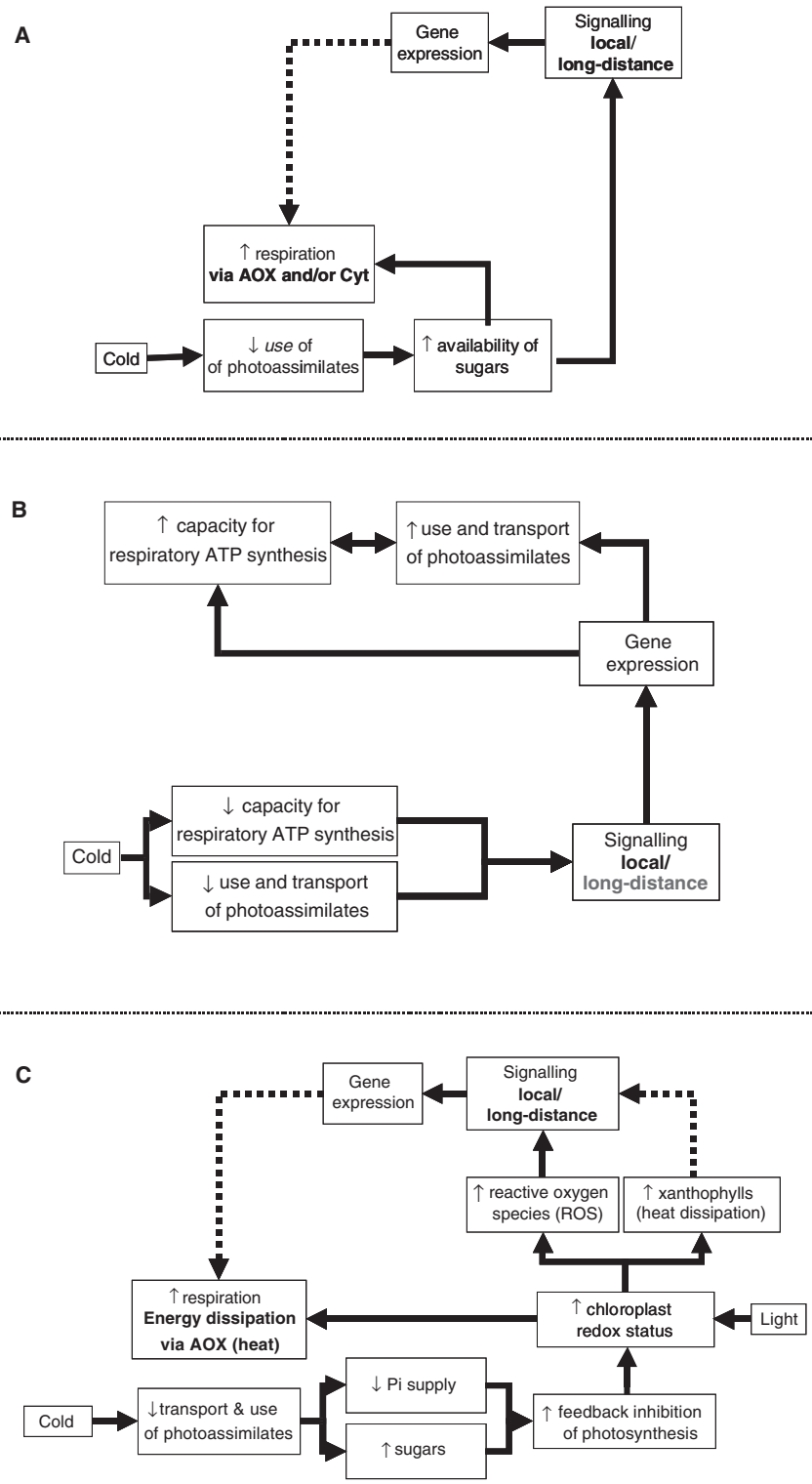

Fig. 6. Schematic diagrammes to indicate the possible mechanisms by which respiration acclimates to low temperatures. In *A*, increases in *R* associated with cold acclimation are the result of increased substrate availability, whereas in *B* cold acclimation of *R* is associated with an increased demand for ATP following acclimation of the processes that use ATP. In *C*, respiratory acclimation is associated with an increased need for energy dissipation, with changes in reactive oxygen species (ROS) being the trigger for the acclimation process. AOX, alternative oxidase; Cyt, cytochrome pathway. Dotted lines indicate less fully elucidated links between model components.

between substrate production and supply is altered, which in turn results in a change in the steady-state concentration of respiratory substrate (e.g. Atkin *et al*. 2000*b*). In tissues where *R* is substrate limited, such changes in substrate availability may alter rates of *R* (e.g. cold acclimation often results in an increase in leaf and root soluble sugar concentrations and concomitant increases in *R*; Tjoelker *et al*. 1999*b*; Atkin *et al*. 2000*b*; Covey Crump *et al*. 2002). Changes in soluble sugar concentrations may also affect gene expression (Sheen 1994; Koch 1996), either locally or in remote tissues as a result of systemic signalling, resulting in enhanced mitochondrial transcript and protein levels (Fig. 6*A*). This may explain, in part, why respiratory capacity appears to be greater in cold acclimated tissues than their warm-grown counterparts. Whether substrate-dependent changes in respiratory flux are coupled to the synthesis of ATP depends, however, on the relative partitioning of electrons between the alternative oxidase (AOX) and cytochrome pathway, as well as the extent to which protons diffuse through the inner mitochondrial membrane through plant uncoupling mitochondrial proteins (PUMP). As PUMP protein (Nantes *et al*. 1999) and AOX protein / engagement (Vanlerberghe and McIntosh 1992; Gonzàlez-Meler *et al*. 1999) increase in cold-acclimated tissues, it seems likely that a portion of the increased capacity is not coupled to the production of ATP.

(2) *Responding to the demand for ATP*. Thermal acclimation may also be linked to ATP demand and synthesis (Fig. 6*B*; Kurimoto *et al*. 2004*a*, *b*). Upon initial exposure to a new growth temperature, demand for ATP will be altered as a result of temperature-dependent changes in the rate of growth, maintenance processes and / or ion uptake. Consequently, temperature-mediated changes in *R* might result from concomitant changes in adenylate restriction of glycolysis and / or mitochondrial electron transport (Atkin *et al*. 2000*a*, *d*; Atkin and Tjoelker 2003). Moreover, at very low temperatures, limitations in the V_{max} of respiratory enzymes can limit potential rates of ATP synthesis (Atkin and Tjoelker 2003). However, both the demand for ATP and ability to synthesise ATP (through increases in cytochrome pathway proteins) could recover following long-term exposure to a new growth temperature (Kurimoto *et al*. 2004*b*). For example, rates of ion uptake and growth often recover (either partially or fully) following a change in growth temperature (e.g. Bigot and Boucaud 1996; Clarkson *et al*. 1988; Ziska and Bunce 1998). If so, this will re-establish a demand for ATP similar to the demand before the change in growth temperature. Changes in the demand for ATP by processes associated with photosynthetic thermal acclimation (e.g. sucrose synthesis) and general maintenance processes could also contribute (Hoefnagel *et al*. 1998; Atkin *et al*. 2000*d*). To meet an increased demand for ATP, respiratory flux can be increased through removal of adenylate restriction of glycolysis and the mitochondrial electron transport chain (at complexes I, III and IV), particularly in tissues where flux is not limited by respiratory capacity. However, whenever the V_{max} of respiratory enzymes limits ATP synthesis (e.g. in the cold; Atkin and Tjoelker 2003), increases in respiratory capacity are necessary; the greater respiratory capacity exhibited by cold-acclimated plants may, therefore, partly reflect changes in gene expression triggered by the increased demand for ATP following acclimation of growth, maintenance and / or ion uptake to the cold (Fig. 6*B*). Variations in the degree of acclimation might, therefore, reflect inter and intra-specific differences in the extent to which growth and maintenance processes maintain a homeostatic demand for ATP (Fig. 6*B*); support for this hypothesis comes from recent work by Kurimoto *et al*. (2004*a*, *b*) which shows that plants capable of maintaining growth at similar rates across a wide range of temperatures also exhibit higher degrees of acclimation than their less flexible counterparts.

(3) *Reducing the production of reactive oxygen species.* imbalances in cellular redox potential (and thus levels of ROS) are another factor that may contribute to variations in the degree of acclimation. ROS is known to be an important signalling agent, both at the site of ROS production (Wagner 1995; Foyer *et al*. 1997) and in remote parts of the plant (Karpinski *et al*. 1999). Wagner (1995) proposed that any constraint on the respiratory electron transport chain [e.g. low temperature inhibition of the cytochrome pathway by cold (Prasad *et al*. 1994)] would lead to increased ROS production. ROS could signal for increased synthesis of enzymes that lower ROS production [e.g. AOX and PUMP (Møller 2001)]. If correct, this suggests that variations in the degree of acclimation might reflect variations in ROS production, which in turn may reflect differences in the environmental cues that lead to ROS production (e.g. irradiance / temperature combinations; Fig. 6*C*).

The potential for ROS production by chloroplasts and mitochondria increases at low temperatures due to over-reduction of the photosynthetic and respiratory electron transport chains (Purvis and Shewfelt 1993; Purvis 1997; Foyer and Noctor 2000; Møller 2001). In illuminated chloroplasts, cold decreases the turnover of NADPH with the result that the photosynthetic electron transport chain becomes highly reduced and ROS production increases (Fig. 6*C*; Fryer *et al*. 1998). Similarly, low temperature inhibition of electron transport through the respiratory electron transport chain may increase the potential for mitochondrial ROS production (Purvis and Shewfelt 1993; Møller 2001). Regardless of the site of ROS production, low temperature-mediated increases in ROS production could be alleviated, in part, by increases in respiratory capacity, particularly through increases in flux through non-phosphorylating pathways such as the AOX (Purvis and Shewfelt 1993). Dutilleul *et al*. (2003) reported that there is effective crosstalk between mitochondria and other organelles to maintain homeostasis of cellular redox

potential. Maxwell *et al*. (1999) showed that overexpression of the AOX decreased the ROS by half, whereas antisensing the AOX increased the production of ROS 5-fold. Similarly, inhibition of the AOX increased ROS production in isolated mitochondria (Popov *et al*. 1997). Increases in AOX thus help avoid over-reduction of the respiratory electron transport chain and the production of mitochondrial derived ROS. However, increases in AOX also appear to reduce the redox potential of the chloroplast. For example, several studies have shown that mitochondria can oxidise excess photosynthetic redox equivalents (Saradadevi and Raghavendra 1992; Shyam *et al*. 1993; Raghavendra *et al*. 1994; Hurry *et al*. 1995); this is achieved through the chloroplast to mitochondrion malate / oxaloacetate (OAA) shuttle mechanism (see Hoefnagel *et al*. 1998). However, for this system to operate successfully in the cold, respiratory flux needs to increase in response to the increased demand for oxidation of redox equivalents. In particular, AOX levels must not be limiting (this may explain why AOX protein levels increase in cold-acclimated leaves; e.g. Vanlerberghe and McIntosh 1992). Thus, Type II acclimation in cold-grown plants may, in part, represent a mechanism to increase the capacity for oxidation of redox equivalents and in turn decrease the potential for ROS generation (Fig. 6*C*).

Impact of acclimation on the balance between respiration and photosynthesis

What impact does thermal acclimation have on the balance between R and photosynthesis? In individual leaves, the short-term temperature sensitivity of light-saturated P (P_{sat}) typically differs from that of leaf R (in darkness). For example, a decline in temperature from 25°C to 15°C reduces leaf R and P_{sat} by 55% and 21%, respectively, in *Eucalyptus pauciflora* (Atkin *et al*. 2000*c*). As a result, the balance between dark leaf R and P_{sat} varies with short-term changes in temperature. However, prolonged exposure to a new growth temperature can result in photosynthetic and respiratory acclimation, with the result that the balance between leaf R and P_{sat} is re-established (Dewar *et al*. 1999; Gifford 1995, 2003; Loveys *et al*. 2003). The maintenance of a balance probably reflects the fact that dark leaf R and P_{sat} are interdependent, with R in darkness relying on photosynthesis for substrate, whereas photosynthesis depends on R in darkness and in the light for a range of compounds, such as carbon skeletons for protein synthesis and ATP for sucrose synthesis and repair of photosynthetic proteins; (Krömer 1995, Hoefnagel *et al*. 1998, Atkin *et al*. 2000*c*, Padmasree *et al*. 2002). What is surprising, however, is the extent to which contrasting species often exhibit similar leaf R to P_{sat} ratios, at least when grown and measured at moderate-high temperatures (e.g. 18, 23 and 28°C; Loveys *et al*. 2003). Leaves of plant species from contrasting habitats differ substantially in chemical composition, metabolic fluxes and physical structures; such differences might result in differences between species and growth temperature in the amount of leaf R needed to support photosynthesis and vice versa. Thus, even though the relationship between leaf R and P_{sat} is affected by environmental factors such as water availability (Turnbull *et al*. 2001), the available data suggests that temperature-mediated differences in dark leaf R are closely linked to concomitant differences in leaf P. Further research such as that by Zha *et al*. (2004) is needed to test this idea in natural variable conditions in the field, where photosynthesis under ambient irradiance instead of P_{sat} is measured.

Does acclimation result in the proportion of daily fixed carbon released by respiratory activity in whole plants being constant across a range of growth temperatures (when measured at the growth temperature)? Few studies have actually measured *in situ* rates of whole plant R and P. Gifford (1995) found that R/P was constant for wheat (*Triticum aestivum)* grown at constant temperatures ranging from 15 to 30°C (when measured at the respective growth temperatures). Likewise, soybean (*Glycine max*) grown at a range of growth temperatures between 20 and 35°C showed no differences in R/P ratios, owing to acclimation of R to temperature (Ziska and Bunce 1998). However, in that study, growth under an elevated concentration of CO_2 (700 μmol mol^{-1}) did result in reduced R/P, compared with growth at ambient CO_2 (350 μmol mol^{-1}). A study of seedlings of five boreal tree species (Tjoelker *et al*. 1999a) showed small increases in the proportion of daily fixed carbon used in R in plants grown in warmer compared with colder growth environments. For example, total R ranged from 24 to 55% of total daily CO_2 uptake amongst species grown at 18 / 12°C, and increased to 38–74% in plants grown at 30 / 24°C. However, the increases were less than would have occurred without acclimation of both respiration and photosynthesis to growth temperature. Moreover, in that study species differed in overall R losses as a proportion of daily net CO_2 uptake. Compared with the faster-growing broad-leaved species *Populus tremuloides* and *Betula papyrifera*, slower-growing conifers *Larix laricina*, *Pinus banksiana*, and *Picea mariana* used a larger proportion of net daily CO_2 uptake in R, especially in roots.

Although R/P in whole plants is often homeostatic at moderate growth temperatures, changes can occur when plants are grown at unfavourably high temperatures. For example, although Loveys *et al*. (2002) found no difference in balance between daily whole plant R and P amongst *Silene uniflora* grown at 18, 23 and 28°C, four other species did exhibit higher daily whole plant R/P values at 28°C than at 18 and 23°C. R/P is also unlikely to remain homeostatic when plants are grown at very low temperatures. Why? First, R and P do not exhibit identical temperature responses when initially exposed to low temperatures (e.g. Atkin *et al*. 2000*c*) and second, R and P may differ in their ability to acclimate to low temperatures. For example, P exhibits greater acclimation to the cold than does leaf R in *Plantago major* (OK Atkin, I Scheurwater, TL Pons unpublished data).

Concluding statements

Our review has highlighted the evidence, including long-standing evidence, that challenges widely held assumptions about the temperature sensitivity of plant *R*, namely that the Q_{10} is around 2.0, that the Q_{10} remains constant, and that *R* response through time in contrasting thermal environments can be described by a simple exponential model. We have shown that the sensitivity of plant *R* to short- and long-term changes in temperature is highly variable and that to successfully model future rates of *R* at a range of scales from individual leaves to global carbon cycle models, factors such as the temperature dependence of the Q_{10} and degree and speed of acclimation will likely need to be taken into account. An example of how this can be done is provided in Wythers *et al*. (2005), where the ecosystem model PnET was run with a temperature driven algorithm that accounts for thermal acclimation and a temperature-dependent Q_{10} algorithm; incorporation of these algorithms resulted in large decreases in predicted annual foliar respiration and increases in predicted net primary productivity, especially in the context of both respiratory and photosynthetic acclimation to temperature and resulting *R* / *P* ratios.

Much is now known about the extent to which Q_{10} values vary and the underlying mechanisms responsible for that variability. For example, whereas Q_{10} does not appear to respond to elevated atmospheric CO_2 concentrations, temperature, light, and water availability each appear to influence the temperature sensitivity of respiratory CO_2 efflux. Moreover, there is growing evidence that the response of *R* to long-term changes in temperature is highly dependent on the effect of temperature on plant development. It seems likely that variations in the degree of acclimation will also reflect interactive effects of temperature and other abiotic factors (e.g. irradiance, drought and nutrient availability). In some cases acclimation may simply reflect a passive response to changes in respiratory substrate availability whereas in others acclimation may be critical in helping plants grow/survive at contrasting temperatures. Much work is needed, however, before we have a full understanding of the factors that determine the extent of thermal acclimation in plants. Establishing what determines the degree of acclimation is critical if we are to successfully predict future rates of *R*, ecosystem CO_2 fluxes and potential feedbacks on atmospheric CO_2 concentrations.

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