Journal of Experimental Botany, Vol. 57, No. 2, pp. 267–281, 2006
Phenotypic Plasticity and the Changing Environment Special Issue
doi:10.1093/jxb/erj029 Advance Access publication 21 December, 2005

Journal of Experimental Botany

Phenotypic plasticity and growth temperature: understanding interspecific variability

O. K. Atkin[1,*], B. R. Loveys[1,2], L. J. Atkinson[1] and T. L. Pons[3]

[1] *Department of Biology, University of York, PO Box 373, York YO1 5YW, UK*

[2] *Ecosystem Dynamics, Research School of Biological Sciences, The Australian National University, GPO Box 475, Canberra, ACT 2601 Australia*

[3] *Department of Plant Ecophysiology, Utrecht University, PO Box 80084, 3508 TB Utrecht, The Netherlands*

Received 27 May 2005; Accepted 25 October 2005

Abstract

The subject of this review is the impact of long-term changes in temperature on plant growth and its underlying components. The discussion highlights the extent to which thermal acclimation of metabolism is intrinsically linked to the plasticity of a range of biochemical and morphological traits. The fact that there is often a trade-off between temperature-mediated changes in net assimilation rates (NAR) and biomass allocation [in particular the specific leaf area (SLA)] when plants are grown at different temperatures is also highlighted. Also discussed is the role of temperature-mediated changes in photosynthesis and respiration in determining NAR values. It is shown that in comparisons that do not take phylogeny into account, fast-growing species exhibit greater temperature-dependent changes in RGR, SLA, and NAR than slow-growing plants. For RGR and NAR, such trends are maintained within phylogenetically independent contrasts (i.e. species adapted to more-favourable habitats consistently exhibit greater temperature-mediated changes than their congeneric counterparts adapted to less-favourable habitats). By contrast, SLA was not consistently more thermally plastic in species from favourable habitats. Interestingly, biomass allocation between leaves and roots was consistently more plastic in slow-growing species within individual phylogenetically independent contrasts, when plants were grown under contrasting temperatures. Finally, how interspecific variations in NAR account for an increasing proportion of variability in RGR as growth temperatures decrease is highlighted. Conversely, SLA played a more dominant role in determining interspecific variability in RGR at higher growth temperatures; thus, the importance of SLA in determining interspecific variation in RGR could potentially increase if annual mean temperatures increase in the future.

Key words: Acclimation, biomass allocation, growth analysis, net assimilation rate, plasticity, photosynthesis, respiration, specific leaf area, temperature.

Introduction

Being sessile organisms, plants experience large temporal variations in temperature; moreover, large spatial variations in temperature are commonly experienced (Larcher, 2004). Variations in temperature affect metabolic processes that contribute to biosynthesis and cellular maintenance (e.g. photosynthesis and respiration; Berry and Raison, 1981). Biomass allocation is also temperature sensitive, with long-term exposure to low temperatures resulting in plants exhibiting a reduced investment in the shoot, and leaves that are thicker and display less leaf area per unit mass than their warm-grown counterparts (Fig. 1; Potter and Jones, 1977; Woodward, 1979*a*; Friend and Woodward, 1990; Williams and Black, 1993; Körner, 1999; Bruhn *et al.*, 2000; Loveys *et al.*, 2002). Collectively, such responses result in the relative growth rate (RGR, rate of increase in dry mass per unit starting mass and time) of individual plants being temperature dependent (Blackmann *et al.*, 1955; Potter and Jones, 1977; Ackerly *et al.*, 1992; Loveys *et al.*, 2002; Hendrickson *et al.*, 2004; Storkey, 2004). Given that the temperatures experienced by plants are changing as a result

* To whom correspondence should be addressed. Fax: +44 (0)1904 328505. E-mail: OKA1@york.ac.uk
Abbreviations: CC, carbon concentration; CV, coefficient of variation; *P*, net photosynthesis; PIC, phylogenetically independent contrast; NAR, net assimilation rate; RGR, relative growth rate; RMR, root mass ratio; LMR, leaf mass ratio; SLA, specific leaf area; *R*, respiration.

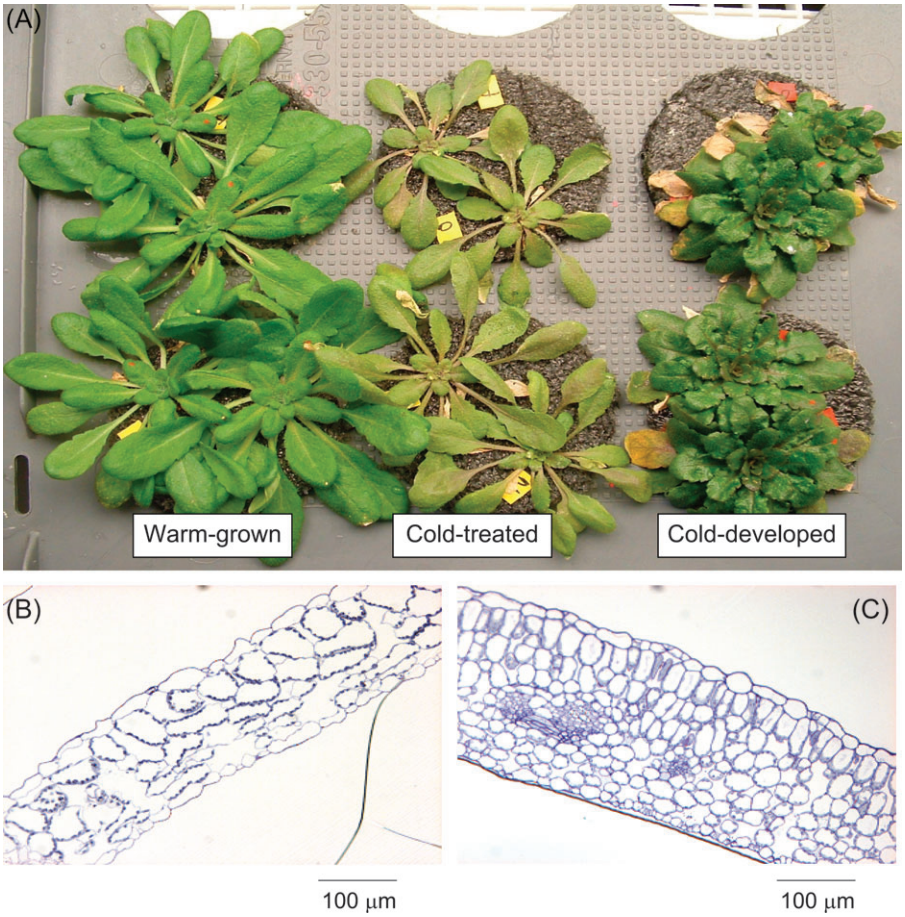

Fig. 1. (A) Examples of warm-grown (left) 10-d-old cold-treated (centre) and cold-developed (right) shoot phenotypes of hydroponically grown *Arabidopsis thaliana* ecotype Columbia. Warm-grown plants experienced 25/20 °C day/night temperatures, whereas cold-treated and cold-developed plants were exposed to constant 5 °C. Cold-developed plants had been exposed to 5 °C for ~50 d following initial 4 weeks of growth at 25/20 °C. (B, C) Transverse sections of representative warm-grown (B) and cold-developed leaves (C). Note the increased overall leaf thickness, increased number of cell layers, and decreased cell size in cold-developed leaves. Scale bars=100 μm. Photograph in (A) courtesy of Peter Gorsuch.

of global climate change (Hulme, 1999; Schimel *et al.*, 2001), predicting the response of plant growth to temperature is fundamental to projecting the impact of global change on the biosphere (Long and Hutchin, 1991).

This paper reviews the impacts of long-term changes in temperature on plant growth and its underlying components. First, the extent to which individual traits are altered following long-term exposure to contrasting temperatures is considered; the paper focuses on the extent to which some traits exhibit plastic responses to growth temperature, and the degree to which plasticity of those traits contributes to thermal acclimation of metabolism, and rates of growth in plants experiencing contrasting growth temperatures; highlighted is the tight coupling that exists between phenotypic plasticity and metabolic acclimation. The impacts of growth temperature on the underlying components of RGR [e.g. the net assimilation rate (NAR), specific leaf area (SLA), and leaf mass ratio (LMR)] are discussed. As part of this section, published data sets (Loveys *et al.*, 2002, 2003*b*) are re-analysed to illustrate the changes to the components of plant growth that can occur when plants are grown at 18 °C, 23 °C, and 28 °C. The importance of respiratory responses to temperature in determining the response of RGR to growth temperature is highlighted. An assessment is then made whether there are systematic differences among contrasting species (e.g. inherently fast- versus slow-growing species) in thermal plasticity of growth-related traits. Here, the data sets of Loveys *et al.* (2002, 2003*a*, *b*) that previously did not take phylogeny into account, but which nevertheless contain several sets of phylogenetically independent contrasts (PICs) (Westoby, 2002) along gradients of environmental favourability (altitude, rainfall, nutrient availability) have been used again. Finally, the impact of interspecific differences in thermal plasticity on the relationship between RGR and its underlying components is considered in a wide range of contrasting species (in the absence and presence of phylogenetic correction). It is shown that irrespective of whether phylogeny is taken into account or not, changes in growth temperature alter the relationship between RGR and its underlying components (the roles of SLA and NAR in

determining interspecific variability in RGR increased and decreased, respectively, at higher growth temperatures).

Phenotypic responses to growth temperature

Plasticity and acclimation

The impact of long-term changes in temperature on plant growth depends, in part, on the 'phenotypic plasticity' of traits underpinning the growth response when plants experience a change in growth temperature. For the purposes of this review, 'phenotypic plasticity' is defined as the capacity for traits within an individual to exhibit a diverse range of phenotypes in response to growth at different temperatures (based on previous definitions by Bradshaw, 1965; Piersma and Drent, 2003; Strand and Weisner, 2004). A good example of phenotypic plasticity to growth temperature is the contrasting leaf structure/morphology exhibited by warm- and cold-grown plants (Fig. 1). In fully expanded, mature leaves, such contrasting phenotypes are largely fixed irrespective of the growth temperature that the plant subsequently experiences [i.e. such plasticity is irreversible; Piersma and Drent (2003) defined such cases as 'developmental plasticity']. By contrast, reversibility is possible in traits that exhibit 'phenotypic flexibility' (Piersma and Drent, 2003). Phenotypic flexibility encompasses molecular and biochemical changes that contribute to changes in the capacity of physiological processes (see next section) within fully expanded tissues that experience changes in growth temperature. In subsequent sections, examples of both forms of phenotypic plasticity are provided.

An important consequence of the wide range of changes associated with temperature-mediated phenotypic plasticity is that the capacity of key metabolic processes often differs between plant tissues with a cold- and warm-grown phenotype. For example, cold-grown plants typically exhibit greater photosynthetic and respiratory capacities than their warm-grown counterparts. As a result, *in situ* rates of metabolism are often similar in plants experiencing contrasting growth temperatures, when measured at their respective growth temperatures (i.e. metabolism 'acclimates'; Körner and Larcher, 1988; Stitt and Hurry, 2002; Atkin and Tjoelker, 2003). Acclimation of metabolism can result in ratios of respiration to photosynthesis (*R*:*P*) being similar in plants experiencing contrasting growth temperatures (Gifford, 1995; Ziska and Bunce, 1998; Dewar *et al.*, 1999; Loveys *et al.*, 2002, 2003*a*; Atkin *et al*. 2005*a*, *b*). Ultimately, the changes associated with phenotypic plasticity can also lead to RGR remaining relatively constant across contrasting growth temperatures (see below).

Although acclimation of photosynthesis and respiration to a new growth temperature can occur in pre-existing leaves formed at the previous growth temperature (Pisek *et al.*, 1973; Loveys *et al.*, 2003*a*) (an example of phenotypic flexibility), data from studies using short-lived herbaceous species suggest that full acclimation to a new growth temperature requires that leaves need to be formed at the new growth temperature (Hurry *et al.*, 1995; Strand *et al.*, 1997; Loveys *et al.*, 2003*a*; Talts *et al.*, 2004; Atkin *et al.*, 2005*b*); thus, the changes associated with developmental plasticity result in greater apparent acclimation of metabolism than do the changes associated with phenotypic flexibility. In addition to increased thickness (Fig. 1), cold-developed leaves exhibit increased levels of membrane lipid unsaturation (Berry and Raison, 1981), contain higher nitrogen concentrations (Ryan, 1995; Tjoelker *et al.*, 1999*b*), have higher transcript and activity levels of photosynthetic and sucrose synthesis enzymes (Hurry *et al.*, 2001), and decreased potential for inorganic phosphate-mediated feedback inhibition of photosynthesis (Strand *et al.*, 1997, 1999) than their warm-grown counterparts. Underpinning many of the acclimation-related changes in metabolism are changes in expression of several cold-responsive genes; these include *CBF/DREB1*, the family of *COR* genes, and the *HOS* genes (Thomashow, 2001; Zarka *et al.*, 2003; Knight *et al.*, 2004). Collectively, such responses enable photosynthesis to operate at similar rates in the cold compared with leaves grown and measured at warmer temperatures (Hurry *et al.*, 2001).

Like photosynthesis, acclimation of respiration to contrasting growth temperatures is closely linked to changes in development and chemical composition (Atkin and Tjoelker, 2003; Atkin *et al.*, 2005*a*, *b*). Cold-developed plants often exhibit enhanced respiratory rates both at low and high temperatures (Atkin *et al.*, 2000*a*; Talts *et al.*, 2004), reflecting an increase in both the density of mitochondria per unit tissue mass and an increase in potential rates of respiratory activity per unit mitochondrial volume (Klikoff, 1966, 1968; Miroslavov and Kravkina, 1991; Armstrong *et al.*, 2005). The abundance of individual proteins/protein complexes and the capacity of terminal oxidases (e.g. alternative and cytochrome oxidase) are also altered in tissues developed at contrasting temperatures (Ribas Carbó *et al.*, 2000; Kurimoto *et al.*, 2004*b*; Armstrong *et al.*, 2005). Importantly, the available data suggest that pre-existing leaves and roots of short-lived species are unable to alter their structure (i.e. anatomy/morphology), chemical composition, and enzymatic capacity to the degree required for full acclimation of respiration to occur; examples are provided in Loveys *et al.* (2003*a*). Further work is needed, however, to assess whether the same is true for slower-growing, longer-lived species.

Underlying components of RGR: responses to temperature

One way of assessing the effects of long-term exposure on plants is to quantify the impact of temperature on RGR and its underlying components [i.e. NAR (the increase in plant mass per unit leaf area and time), SLA (the ratio of leaf area to leaf dry mass), and LMR (ratio of leaf mass to plant

mass)]. NAR largely reflects the rate of whole-plant photosynthetic carbon gain minus carbon released by respiration (Lambers and Poorter, 1992). RGR is related to these parameters according to:

$$\mathrm{RGR} = \mathrm{NAR} \times \mathrm{SLA} \times \mathrm{LMR} \quad (1)$$

Short-term changes in temperature have their immediate impact on RGR via changes in NAR, which in turn is dependent on the temperature response of photosynthesis and respiration (Forward, 1960; Berry and Björkman, 1980; Atkin *et al.*, 2005*a*) according to:

$$\mathrm{NAR} = (P_a - R_a)/\mathrm{CC} \quad (2)$$

where P_a is daily whole shoot net photosynthesis per unit leaf area, R_a is whole plant respiration per unit area, and CC is whole plant carbon concentration. R_a is the sum of root respiration over a 24 h period plus shoot respiration during the night (both expressed on a leaf area basis). R_a is related to rates of whole plant respiration per unit mass (R_m), SLA and LMR according to:

$$R_a = R_m/(\mathrm{SLA} \times \mathrm{LMR}) \quad (3)$$

Changes in R_a that occur following short-term changes in temperature will be almost entirely due to temperature-dependent changes in R_m, due to the fact that neither SLA or LMR will undergo substantial change over short-time periods. However, the biomass allocation parameters (SLA and LMR) could play a greater role following longer-term changes in temperature.

Recently, a growth analysis was conducted on large *Arabidopsis thaliana* (Col-0) plants shifted from 25 °C to 5 °C (OK Atkin, LJ Atkinson, unpublished results); RGR decreased from 75 mg g^{-1} d^{-1} to near 0 mg g^{-1} d^{-1}, due to an immediate drop in the NAR (brought about by a large decline in P_a). However, RGR subsequently recovered to 30 mg g^{-1} d^{-1} [due to metabolic changes within pre-existing tissues and alterations in the phenotype of newly formed, cold-developed tissues (Fig. 1), which collectively resulted in a decrease in the SLA and an increase in NAR]. Similar homeostatic adjustments in RGR are reported for plants grown over a wide range of temperatures (Tjoelker *et al.*, 1998*b*; see Table 1), due to temperature-mediated changes in NAR, LMR, and/or SLA. Because long-term changes in temperature often result in adjustments in all parameters underpinning the RGR, the linkage between NAR and RGR is often less clear in plants exposed to contrasting temperatures for extended periods than it is in plants experiencing short-term changes in temperature (Blackmann *et al.*, 1955; Stirling *et al.*, 1998; Bruhn *et al.*, 2000). To illustrate further how long-term differences in growth temperature impact on RGR and its underlying components (see equation 1), the mean values for 16 contrasting species grown at 18 °C, 23 °C, and 28 °C, using data reported by Loveys *et al.* (2002, 2003*b*), were calculated for several growth-related traits. Table 2 shows that growth at 18 °C and 23 °C had little impact on the average RGR of all species and that average RGR was substantially reduced when plants were grown at 28 °C. Between 18 °C and 23 °C, RGR remained relatively constant due to decreases in NAR being largely offset by increases in SLA. Above 23 °C, RGR declined largely due to decreases in NAR.

An example of plastic changes in biomass allocation are temperature-dependent changes in the relative investment in above- and below-ground organs, particularly when leaves and roots experience contrasting growth temperatures (Kummerrow and Ellis, 1984; Clarkson *et al.*, 1986; DeLucia *et al.*, 1992; Körner, 1999; Weih and Karlsson, 2001; Cunningham and Read, 2003) (for examples of root: shoot ratios, see Table 1). However, when roots and leaves experience equal temperatures in a controlled environment, in which plants are grown hydroponically, other reports have found LMR to be temperature insensitive (Tjoelker *et al.*, 1998*b*; Loveys *et al.*, 2002). An example is shown in Table 2, which provides mean values for 16 contrasting species grown at 18 °C, 23 °C, and 28 °C, using LMR data reported by Loveys *et al.* (2002). It seems that temperature-mediated changes in LMR are more likely in cases where leaf and roots experience contrasting temperatures.

How plastic is biomass allocation within leaves (i.e. SLA) in plants grown under contrasting temperature regimes? Analysis of the Loveys *et al*. (2002) data set demonstrates that average SLA values were lowest at 18 °C, with 23 °C and 28 °C exhibiting relatively similar average SLA values; average SLA at 18 °C was 31% lower than that at 28 °C (Table 2). Similar temperature-dependent changes in SLA were reported by Williams and Black (1993), when they grew *Pennisetum setaceum* (a grass introduced to Hawaii) at two temperatures (Table 1). Moreover, Woodward (1979*a*, *b*) found that SLA of both alpine and lowland plants decreased with decreasing growth temperature (Table 1). By contrast, Hovenden (2001) found no difference in SLA values between southern beech seedlings grown at 23 °C and 18 °C. Tjoelker *et al.* (1998*b*) also reported no systematic temperature-induced change in SLA values of five deciduous and evergreen tree species grown at five temperatures (Table 1). The impact of temperature on SLA therefore depends on which species is being investigated and the temperature regimes at which the plants are grown.

The response of NAR to long-term differences in growth temperature is highly variable in published studies. For example, in a comparison of four rainforest canopy species grown under controlled conditions (14/6 °C, 19/11 °C, 22/14 °C, 25/17 °C, and 30/22 °C day/night temperatures), Cunningham and Read (2003) found that NAR increased with increasing growth temperature, whereas Tjoelker *et al*. (1998*b*) reported that NAR values were often similar in tree seedlings grown at five temperatures (Table 1). NAR also exhibited little systematic change with growth temperature

Table 1. *Comparison of growth-related traits for a range of species and growth temperatures at ambient CO_2 concentrations*

Abbreviations: RGR, relative growth rate (mg g^{-1} d^{-1}); NAR, net assimilation rate (g m^{-2} d^{-1}); SLA, specific leaf area (m^2 kg^{-1} leaf mass).

Parameter	Species	Temperature regime									Source
RGR (mg g^{-1} d^{-1})		Soil temp	5.9 °C	10.1 °C	15.2 °C	20.2 °C	24.5 °C	29.7 °C	33.9 °C	35.5 °C	
	Andropogon gerardii		70	90	140	170	0.20	0.19	0.18	0.15	DeLucia *et al.* (1992)
			18/12 °C	21/15 °C	24/18 °C	27/2 °C	30/24 °C				
	Populus tremuloides		257	249	183	187	235				Tjoelker *et al.* (1998*b*)
	Betula papyrifera		177	172	139	164	132				
	Larix laricina		70	73	70	70	84				
	Pinus banksiana		56	38	44	46	52				
	Picea mariana		56	38	48	56	56				
			25/13 °C	25/13 °C							
	Pennisetum setaceum		72	77							Williams and Black (1993)
			15 °C	25 °C							
	Wheat cv. Stiletto		184	205							Kurimoto *et al.* (2004*a*)
	cv. Patterson		162	197							
	cv. Brookton		138	193							
	Rice cv. Amaroo		60	135							
NAR (g m^{-2} d^{-1})		Soil temp	5.9 °C	10.1 °C	15.2 °C	20.2 °C	24.5 °C	29.7 °C	33.9 °C	35.5 °C	
	Andropogon gerardii		8.1	12.5	20	24	32.5	27.5	22.5	17.5	DeLucia *et al.* (1992)
			18/12 °C	21/15 °C	24/18 °C	27/21 °C	30/24 °C				Tjoelker *et al.* (1998*b*)
	Populus tremuloides		10.9	7.3	9.1	10.1	12.3				
	Betula papyrifera		8.2	9.2	11.4	8.1	13.0				
	Larix laricina		6.8	7.0	7.5	7.6	7.6				
	Pinus banksiana		4.0	4.8	5.0	5.1	6.2				
	Picea mariana		2.8	5.0	5.2	5.0	5.8				
			15 °C	25 °C							
	Wheat cv. Stiletto		13.0	12.9							Kurimoto *et al.* (2004*a*)
	cv. Patterson		10.7	11.3							
	cv. Brookton		9.7	12.2							
	Rice cv. Amaroo		11.0	9.3							
SLA (m^2 kg^{-1})			10/5 °C	20/5 °C							
	Phleum bertolonii		38	58							Woodward (1979*b*)
	P. alpinum		27	46							
			18/12 °C	21/15 °C	24/18 °C	27/21 °C	30/24 °C				Tjoelker *et al.* (1998*b*)
	Populus tremuloides		35.6	39.9	32.6	39.1	33.6				
	Betula papyrifera		37.1	25.4	26.8	27.4	24.3				
	Larix laricina		16.7	15.9	14.0	17.4	13.9				
	Pinus banksiana		15.3	15.2	15.3	16.7	15.9				
	Picea mariana		19.0	15.2	15.6	17.2	13.2				
			25/13 °C	25/13 °C							
	Pennisetum setaceum		16.1	18.2							Williams and Black (1993)
Root:shoot ratio		Air temp		2 °C			12 °C			22 °C	
		Root temp	2 °C	7 °C	12 °C	2 °C	7 °C	12 °C	2 °C	7 °C	12 °C	
	Eriophorum vaginatum		0.07	0.12	0.14	0.03	0.16	0.38	0.04	0.09	0.24	Kummerow and Ellis (1984)
	Carex bigelowii		0.94	0.78	0.58	0.58	0.96	1.11	0.80	1.16	1.48	
		Soil temp	5.9 °C	10.1 °C	15.2 °C	20.2 °C	24.5 °C	29.7 °C	33.9 °C	35.5 °C	
	Andropogon gerardii		1.0	1.2	2.2	2.4	3.9	2.8	2.5	2.2	DeLucia *et al.* (1992)
		Shoot temp				25 °C					
	Lolium perenne	Root temp	3 °C	5 °C	7 °C	9 °C	11 °C	13 °C	17 °C	25 °C	
			0.12	0.16	0.14	0.19	0.23	0.22	0.27	0.25	Clarkson *et al.* (1986)

Table 2. *Comparison of average values of growth related traits for plants grown at 18 °C, 23 °C, and 28 °C (irradiance 300 μmol photons m^{-2} s^{-1})*

Depending on the parameter, values represent the mean of 12–16 species (±standard error). Data used to construct these graphs was taken from Loveys *et al.* (2002, 2003*b*, *a*) and include grass, forb, shrub, and tree species. Abbreviations: RGR, relative growth rate (mg g^{-1} d^{-1}); NAR, net assimilation rate (g m^{-2} d^{-1}); SLA, specific leaf area (m^2 kg^{-1} leaf mass); LMR, leaf mass ratio (g_{leaf} g_{plant}^{-1}); StMR, stem mass ratio (g_{stem} g_{plant}^{-1}); RMR, root mass ratio (g_{root} g_{plant}^{-1}); CC, carbon concentration (mmol C g^{-1}).

Parameter	Growth temperature		
	18 °C	23 °C	28 °C
RGR	136±17	152±13	118±14
NAR	12.6±1.2	10.6±0.7	7.2±0.5
SLA	16.9±1.5	23.9±1.8	24.4±1.9
LMR	0.65±0.02	0.62±0.02	0.65±0.01
StMR	0.12±0.02	0.12±0.02	0.12±0.01
RMR	0.24±0.02	0.26±0.02	0.23±0.01
CC	34.0±0.50	31.7±0.5	32.0±0.5

in several other species (Stirling *et al.*, 1998; Bruhn *et al.*, 2000; Kurimoto *et al.*, 2004*a*). By contrast, both Bednarz and van Iersel (2001) and Loveys *et al.* (2002) reported that NAR decreased with increasing growth temperature (see Table 2 for a summary of the data of Loveys *et al.*, 2002). In the study by Loveys *et al.* (2002), average NAR values decreased as growth temperatures increased, being 75% higher at 18 °C than at 28 °C (Table 2).

Growth temperature-mediated variations in NAR

What factors might explain the variable response of NAR to growth temperature? As shown in equation 2, NAR is equal to P_a minus R_a divided by CC, with R_a being influenced by both biomass allocation and rates of R_m (equation 3). Given that temperature-sensitive changes in CC are unlikely to account for temperature-induced changes in NAR either in the short- or long-term [rather than being *lower* at low growth temperatures, Loveys *et al.* (2002) found that CC values were actually *highest* in plants grown at the lowest growth temperature (Table 2), particularly in fast-growing species], changes in NAR following long-term exposure to contrasting temperatures must reflect responses of P_a and/or R_a. In the absence of metabolic acclimation or plastic changes in biomass allocation, increases in temperature are expected to decrease NAR (and, conversely, NAR will increase with decreasing temperature), due to respiration being more temperature sensitive than photosynthesis in short-term experiments (Berry and Björkman, 1980). In such cases, the ratio of respiration to photosynthesis increases with increasing temperature (Gifford, 1995; Ziska *et al.*, 1998; Dewar *et al.*, 1999; Atkin *et al.*, 2000*b*). Thus, the fact that NAR is often similar or even greater in plants grown at high temperatures (compared with cool-grown plants; Tjoelker *et al.*, 1998*b*; Cunningham and Read, 2003) suggests that in those studies, P_a and/or R_a must have adjusted to long-term changes in temperature (Tjoelker *et al.*, 1998*a*, 1999*a*). Such adjustment could reflect acclimation of the underlying photosynthetic and respiratory machinery, or plastic changes in biomass allocation (e.g. equation 3). By contrast, less adjustment of P_a and/or R_a is likely in species where NAR decreased markedly with increasing growth temperature. Thus, variations in the temperature response of NAR are likely to reflect the degree to which P_a and R_a adjust to long-term changes in temperature.

Underpinning variations in the degree of acclimation of area-based fluxes could be either changes in rates per unit mass and/or the ratio of leaf area to mass relationships (e.g. as driven by changes in SLA). Theoretically, decreases in SLA (underpinned by increases in leaf thickness) could lead to an increase in NAR due to increases in capacity of the photosynthetic machinery per unit leaf area that result from greater numbers of mesophyll cells and/or abundance of chloroplasts per unit leaf area (Lambers and Poorter, 1992; Shipley, 2000). Examples of temperature-mediated changes in shoot phenotype and leaf structure are provided in Fig. 1, which shows shoots of warm-grown, cold-treated (i.e. warm-grown plants shifted to chilling temperatures for several days) and cold-developed (i.e. leaves produced following a total of 50–60 d chilling treatment) plants, as well as transverse leaf sections of *Arabidopsis thaliana* that developed at 25/20 °C or 5 °C (Armstrong *et al.*, 2005). However, realizing gains from additional photosynthetic capacity requires that leaves be exposed to high irradiance; in leaves exposed to low irradiance, decreases in SLA are unlikely to result in concomitant increases in NAR.

To what extent are lower NAR values in high temperature-grown plants due to increased respiratory losses (i.e. high daily R_a values)? Although Loveys *et al.* (2002) did not measure whole-plant gas exchange in the 16 species shown in Table 2, they did conduct measurements using a sub-set of six species. Averaged across the six species, daily R_a values were nearly identical in plants grown at 18 °C and 23 °C (102 and 109 mmol CO_2 m^{-2} d^{-1}), increasing by nearly 30% to 134 mmol CO_2 m^{-2} d^{-1} in plants grown at 28 °C (Loveys *et al.*, 2002). In the absence of changes in P_a or CC, such changes in R_a alone should decrease NAR by nearly 1.0 g m^{-2} d^{-1} (this calculation was based on the assumption that SLA, LMR, P_a, and CC values remained constant at 24 m^2 kg^{-1}, 0.65 g_{leaf} g_{plant}^{-1}, 540 mmol CO_2 m^{-2} d^{-1}, and 32 mmol C g^{-1}, respectively). Given that NAR was >3.0 g m^{-2} d^{-1} lower at 28 °C than 23 °C (Table 2), this suggests that temperature-mediated reductions in NAR at the high growth temperature must have also been due, in part, to reductions in P_a; indeed, when averaged across the six species, daily whole-shoot P_a values were lower at 28 °C (540 mmol CO_2 m^{-2} d^{-1}) than at 23 °C (583 mmol CO_2 m^{-2} d^{-1}). Thus, alterations in P_a and R_a contribute to differences in NAR at contrasting growth temperatures. In turn, variations in R_a largely reflect

temperature-mediated changes in R_m values rather than changes in biomass allocation (see Loveys *et al.*, 2002).

Temperature-mediated changes in RGR: what underlying factor is more important?

What underlying factors play the dominant role in determining variations in RGR when plants are grown at different temperatures? Although there is often a negative interplay between NAR and SLA, changes in one parameter are often not matched by concomitant changes in the other. An example is shown in Table 2, where increases in NAR at low growth temperature were not fully matched by decreases in SLA; in such cases, temperature-mediated variations in NAR play a more dominant role in determining RGR at each growth temperature than do variations in SLA. This is further illustrated in Fig. 2, where the extent to which RGR remained constant over the 18–23 °C interval (i.e. RGR_{18}/RGR_{23}, RGR at 18 °C divided by RGR at 23 °C) for individual species was plotted against the difference in NAR values at 18 °C and 23 °C (raw data was extracted from Loveys *et al.*, 2002); the ratio RGR_{18}/RGR_{23} was greatest in plants that exhibited the greatest increase in NAR at 18 °C compared with 23 °C. In a study assessing the impact of temperature on growth of three wheat cultivars and rice, Kurimoto *et al.* (2004*a*) also found that temperature-mediated changes in NAR played a prominent role in determining the variations in RGR in plants grown under controlled-environment conditions. Similarly, in a study of 18 annual weed and two crop species, Storkey (2004) found that variations in RGR were largely determined by the NAR in the autumn in plants grown outdoors. However, in spring, variations in the ratio of leaf area to plant mass largely determined the RGR (Storkey, 2004). The linkage between NAR and RGR may thus be dependent on developmental stage or on other factors associated with seasonal changes in the environment.

Taken together, this section highlights how, in response to lower growth temperatures, SLA values decrease with a potential negative effect on RGR. However, acting against this decline in SLA is an increase in the NAR (at least for plants grown under sub-saturating irradiance). Further work is needed to assess whether growth temperature has similar effects on SLA and NAR in plants experiencing higher irradiances and/or lower temperature regimes than those used by Loveys *et al.* (2002).

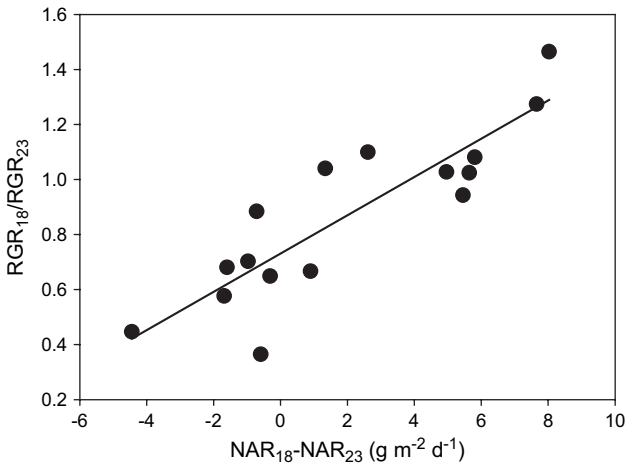

Fig. 2. Relationship between relative growth rate (RGR) of plants grown at 18 °C divided by the RGR of plants grown at 23 °C, and temperature-induced changes in net assimilation rate (NAR, g m^{-2} d^{-1}) (P <0.001, r^2=0.70). Each point represents a different species. Homeostasis of RGR was calculated by dividing RGR values of plants grown at 18 °C by the corresponding RGR of plants grown at 23 °C. The effect of growth temperature on NAR was calculated by subtracting the NAR value of plants grown at 18 °C from the NAR value of plants grown at 23 °C. Data used to construct these graphs were taken from Loveys *et al.* (2003*b*) and include grass, forb, shrub, and tree species.

Systematic differences among species in their response to growth temperature

In the previous section, the extent to which some of the underlying components of RGR exhibit plastic responses when grown at different temperatures, and how acclimation of metabolism is underpinned by plasticity of a range of morphological and biochemical traits was discussed. In this section, consideration is given to whether there are systematic differences among contrasting species (e.g. inherently fast- versus slow-growing species) in the response to growth temperature.

Acclimation of photosynthesis and respiration

Studies investigating the temperature responses of photosynthesis and respiration have found that there is considerable variability in the degree of photosynthetic and respiratory acclimation among species, with some species fully acclimating while others are incapable of even partial acclimation (Berry and Raison, 1981; Larigauderie and Körner, 1995; Xiong *et al.*, 2000; Atkin *et al.*, 2005*a*, *b*). Tjoelker *et al.* (1999*a*) suggested that broad-leaved tree species exhibited a lower degree of acclimation of leaf respiration than selected conifer species; they suggested that it may be possible to predict degrees of acclimation/homeostasis of respiration using structural and/or functional traits. Moreover, in a comparison of thermal acclimation of photosynthesis and leaf respiration in two lowland and one alpine *Plantago* species, Atkin *et al.* (2005*a*) found that only the fast-growing lowland species exhibited significant metabolic acclimation when grown at three different temperatures (13 °C, 20 °C, and 27 °C); moreover, only the lowland species exhibit plasticity of leaf structure in response to growth temperature. Collectively, such results suggest that inherently fast-growing species may indeed be more morphologically plastic and capable of exhibiting greater acclimation/homeostasis of metabolic flux than their slow-growing counterparts. By contrast, other

studies have not found systematic differences in the degree of acclimation of respiration. For example, Larigauderie and Körner (1995) found no systematic differences in thermal acclimation of respiration among alpine and lowland plant species. Moreover, in a comparison of 16 fast- and slow-growing species, Loveys *et al.* (2003*a*) found no systematic difference in respiratory homeostasis of either roots or leaves, when homeostasis/acclimation ratios were plotted against RGR values. Thus, it may be premature to conclude that all fast-growing species are more plastic and capable of exhibiting greater thermal acclimation of respiration than their slow-growing counterparts.

Case study: comparisons of plasticity in contrasting species across all taxa

To assess further whether there are systematic differences in response to growth temperature among the fast- and slow-growing species used by Loveys *et al.* (2002), the absolute difference between the maximum and minimum value of a trait (irrespective at which growth temperature the maximum and minimum values occurred) was calculated (Fig. 3). In comparisons of all taxa (i.e. not taking into account phylogeny), each max–min value against the maximum RGR exhibited by that species across the three growth temperatures was then plotted (Fig. 3). No systematic differences were found in the max–min values of leaf mass ratio (LMR), stem mass ratio (StMR), or root mass ratio (RMR) among fast- and slow-growing species in comparisons of all taxa (data not shown). However, there was a significant positive correlation between max–min values of RGR, SLA, and NAR, and the maximum RGR value exhibited by each species across the three growth temperatures, with the slope being greatest in the NAR_{max}–NAR_{min} versus RGR_{max} plot (Fig. 3B). Thus, although there is no systematic difference among species in how biomass allocation between leaves, stems, and roots respond to growth temperature, fast-growers do exhibit greater absolute changes in RGR, SLA, and NAR than their slow-growing counterparts. Such absolute differences are relevant when considering how growth temperature alters the competitive ability of species (e.g. large absolute induced changes in leaf area may enable a plant to outcompete its neighbours for light).

Importantly, no systematic difference in plasticity of SLA among the fast- and slow-growing species was found when the *relative* ability of an individual species to alter traits (e.g. biomass allocation) was assessed on being challenged with different growth temperatures (Fig. 4). The relative ability to alter SLA was calculated using the percentage coefficient of variation approach (%CV, where CV=100×standard deviation of individual temperature treatment means)/grand mean of the temperature treatment means; Ryser and Eek, 2000; Bloor and Grubb, 2004). Similarly, no systematic differences were found among fast- and slow-growing species in terms of *relative* change in RGR or NAR brought about by differences in growth temperature (not shown). Thus, while growth temperature does have a greater absolute effect on growth parameters of fast-growing species, contrasting species do not appear to differ in plasticity assessed using scales that are relative.

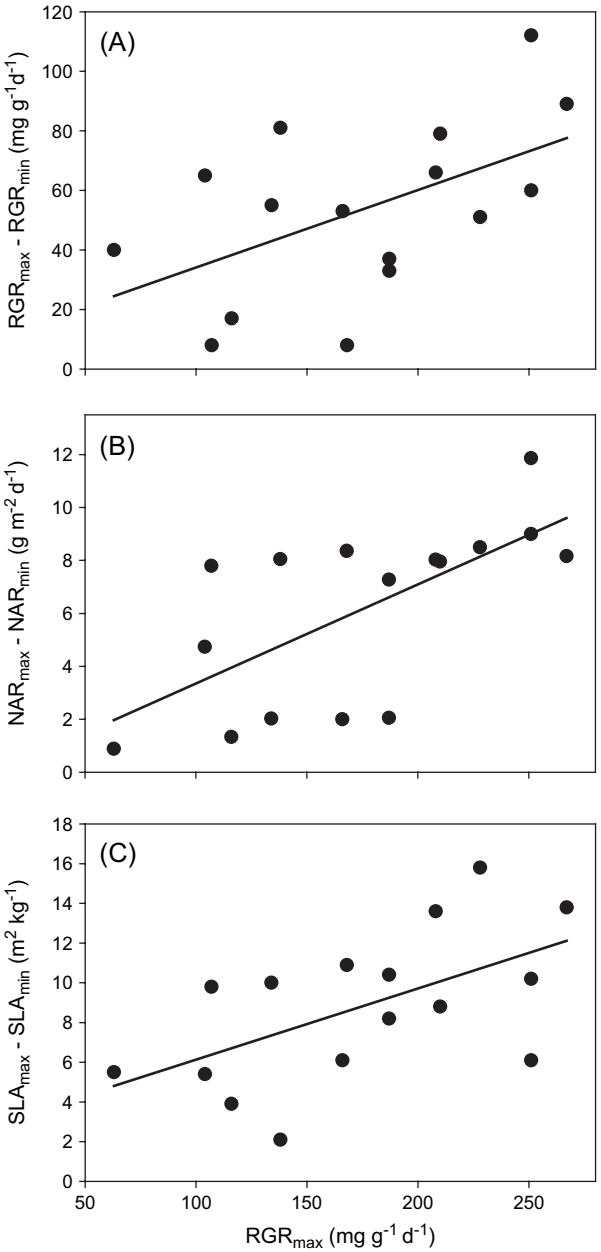

Fig. 3. The absolute difference between maximum and minimum (A) relative growth rate (RGR), (B) net assimilation rate (NAR), and (C) specific leaf area (SLA) values exhibited by 16 species grown at three temperatures (18 °C, 23 °C, and 28 °C) plotted against the maximum RGR value exhibited by each species. Maximum and minimum values exhibited by each species at the three growth temperatures were used, irrespective of which temperature the maximum or minimum value occurred. Data used to construct these graphs were taken from Loveys *et al.* (2003*b*) and include grass, forb, shrub, and tree species. In each graph, the regressions were significant at $P < 0.01$. The r^2 values in (A), (B), and (C) were 0.29, 0.44, and 0.33, respectively.

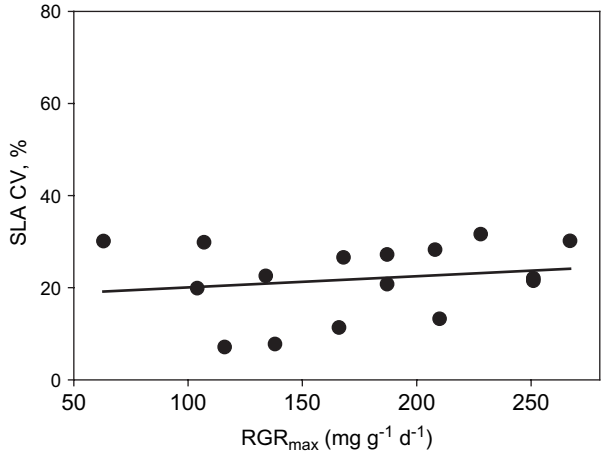

Fig. 4. The percentage coefficient of variation (%CV) among three growth temperatures (18 °C, 23 °C, and 28 °C) for specific leaf area (SLA) values exhibited by 16 species grown at three temperatures (18 °C, 23 °C, and 28 °C) plotted against the maximum RGR value exhibited by each species. %CV was calculated according to %CV=100×standard deviation of individual temperature treatment means)/grand mean of the temperature treatment means, as described elsewhere (Ryser and Eek, 2000; Bloor and Grubb, 2004). Maximum and minimum values exhibited by each species at the three growth temperatures were used, irrespective of which temperature the maximum or minimum value occurred. Data used to construct these graphs were taken from Loveys *et al.* (2003*b*) and include grass, forb, shrub, and tree species.

The data shown in Fig. 3 were for comparisons where phylogeny was not taken into account. Here, it is asked whether those trends across all species (irrespective of phylogeny) also exist within PICs. Each PIC contained a fast- and a slow-growing species characteristic of environmentally favourable and unfavourable habitats, respectively (three nutrient contrasts, two rainfall contrasts, and two altitudinal contrasts). PIC patterns were interpreted in a qualitative manner (Wright and Westoby, 1999), as significance testing would have required greater replication than was available from the data sets of Loveys *et al.* (where data on seven PICs were available); consequently, only majority trends among PICs (five out of seven PICs, six out of seven PICs, or seven out of seven PICs) were considered indicative of a consistent relationship (Wright and Westoby, 1999). Figure 5 shows PIC stick graphs (Westoby *et al.*, 1998) of absolute differences between the maximum and minimum values of a trait (irrespective of which growth temperature the maximum and minimum values occurred) for plant species representative of favourable and unfavourable habitats. Temperature-induced differences in RGR were generally greater in the species characteristic of favourable habitats (in six out of the seven contrasts; Fig. 5A). Only in the genus *Acacia* did the species from the unfavourable habitat (*A. aneura*) respond more dynamically to temperature than the species from a more favourable habitat (*A. melanoxylon*). Similarly, temperature-induced differences in NAR were consistently higher in plants from favourable habitats (Fig. 5B).

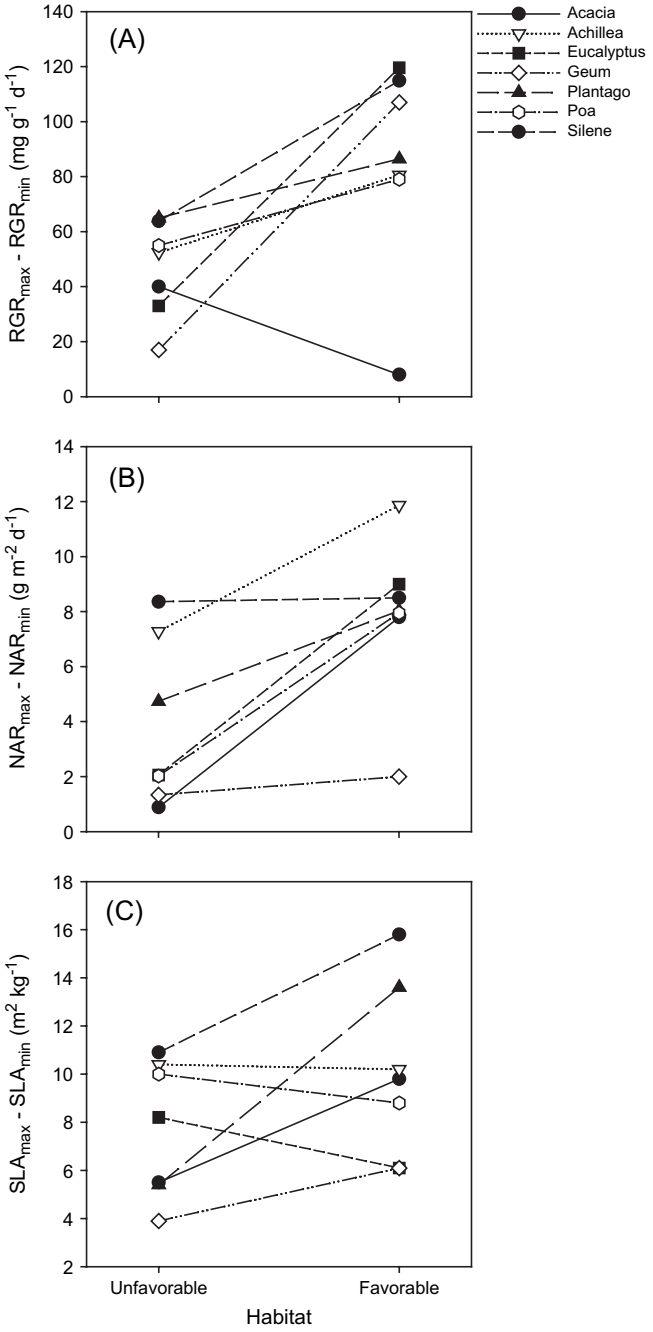

Fig. 5. The absolute difference between maximum and minimum (A) relative growth rate (RGR), (B) net assimilation rate (NAR), and (C) specific leaf area (SLA) values for seven PICs for species characteristic of unfavourable and favourable habitats. Maximum and minimum values exhibited by each species at three growth temperatures (18 °C, 23 °C, and 28 °C) were used, irrespective of which temperature the maximum or minimum value occurred). Data used to construct these graphs were taken from Loveys *et al.* (2003*b*) and include grass, forb, shrub, and tree species.

However, by contrast to the general trends across all species (Fig. 3), species from favourable habitats did not consistently exhibit greater temperature-induced differences in SLA (differences in SLA were only greater in

the species from favourable habitats in four out of the seven contrasts; Fig. 5C). Thus, while temperature-induced changes in RGR and NAR were consistently different in species from contrasting habitats, no such conclusion can be reached for SLA (i.e. adaptation to stressful habitats is not consistently associated with a decrease in thermal plasticity of leaf area to mass relationships). This result is surprising, as it is often assumed that fast-growing species with high SLA values are more plastic than their slow-growing counterparts (Lambers *et al.*, 1998). While this is true when phylogeny is not taken into account (Fig. 3), it is not necessarily the case within individual PICs (Fig. 5C).

Another surprising outcome of the present PIC analysis was that, by contrast to the general trends across all species (see above), consistent differences in plasticity of LMR and RMR to temperature were found within individual PICs (Fig. 6). In the case of LMR, five out of the seven contrasts exhibited greater plasticity of LMR in species from unfavourable habitats. For RMR, the trend was highly consistent, with species from unfavourable habitats exhibiting greater plasticity than their favourable habitat counterparts in seven out of the seven contrasts. Thus, even though temperature has relatively little absolute effect on LMR and RMR (Loveys *et al.*, 2002), and across all taxa there is no systematic difference in plasticity of LMR and RMR among fast- and slow-growing species (see above), consistent differences in plasticity are found within most clades. This suggests that adaptation to stressful, unfavourable habitats is associated with increased plasticity of biomass allocation between leaves and roots in response to differences in growth temperature. One possible explanation for this result is that the nutrient uptake potential of a given unit of root mass varies with growth temperature (e.g. decreasing at lower growth temperatures). To overcome limitations in nutrient uptake at unfavourable temperatures, a plant could either increase the uptake capacity of a given mass of roots, or increase allocation of biomass to roots. It is suggested that in species characteristic of unfavourable habitats, greater reliance is placed on changes in biomass allocation to roots than is the case for species characteristic of more favourable habitats. Further research is needed to determine whether this hypothesis is correct.

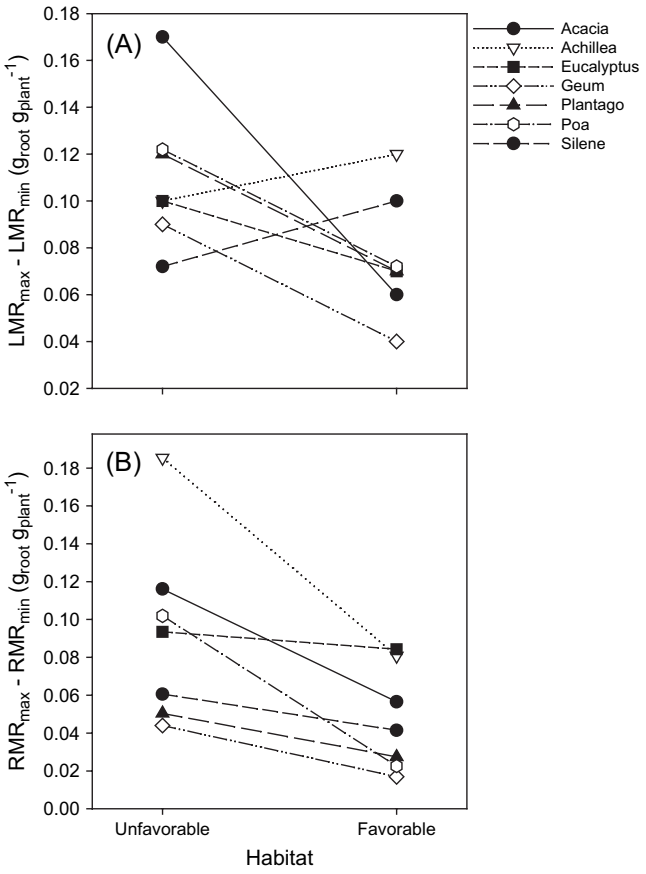

Fig. 6. The absolute difference between maximum and minimum (A) leaf mass ratio (LMR) and (B) root mass ratio (RMR) values for seven PICs for species characteristic of unfavourable and favourable habitats. Maximum and minimum values exhibited by each species at three growth temperatures (18 °C, 23 °C, and 28 °C) were used, irrespective of which temperature the maximum or minimum value occurred. Data used to construct these graphs were taken from Loveys *et al.* (2003*b*) and include grass, forb, shrub, and tree species.

Temperature and relationship between RGR and its underlying components

Trends across all taxa, irrespective of phylogeny

Most of the studies investigating the relationship between inherent differences in RGR and its underlying components have been conducted using plants grown under controlled environmental conditions at a single temperature (Lambers and Poorter, 1992; Poorter and Garnier, 1999). Although both Garnier and Freijsen (1994) and Poorter and De Jong (1999) found that changes in growth environment do not alter the ranking of leaf traits (e.g. SLA) across species, one consequence of interspecific differences in thermal plasticity (see previous section) is that the relationship between RGR and its underlying components in contrasting species varies with growth temperature (Loveys *et al.*, 2002). Loveys *et al.* (2002) found that the importance of SLA for explaining variations in RGR was reduced as growth temperature decreased (Fig. 7). Conversely, variations in NAR played a greater role in determining interspecific differences in RGR in plants grown at 18 °C than in plants grown at 23 °C and 28 °C (Fig. 7). Loveys *et al.* (2002) found that the increasing importance of NAR in determining interspecific differences in RGR as growth temperatures decreased was due to interspecific differences in the degree of thermal acclimation of whole plant respiration (R_a) (with the degree of homeostasis of R_a being greatest in inherently slow-growing species). Rates of whole plant respiration per unit plant mass (R_m) were also more homeostatic (across growth temperatures) in the slow-growing

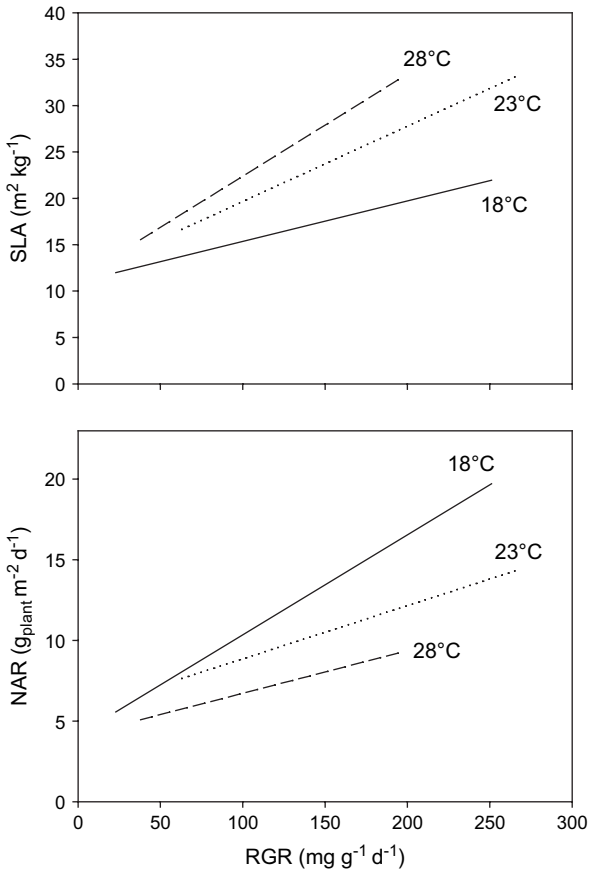

Fig. 7. Impact of growth temperature (18°C, 23°C, and 28°C) on the relationship between relative growth rate (RGR, g g^{-1} d^{-1}) and two of its underlying components: (A) specific leaf area (SLA, m^2 kg^{-1}) and (B) net assimilation rate (NAR, g m^{-2} s^{-1}). Corrected equations for the linear regressions of SLA and NAR versus RGR (Loveys *et al*., 2003*b*) were: SLA_{18}=11.0+0.044×RGR, r^2=0.23; SLA_{23}=11.5+0.081×RGR, r^2=0.37; SLA_{28}=11.4+0.110×RGR, r^2=0.65; NAR_{18}=4.1+0.062×RGR, r^2=0.70; NAR_{23}=5.6+0.033×RGR, r^2=0.38; NAR_{28}=4.1+0.026×RGR, r^2=0.54.

species (Loveys *et al.*, 2002). In a subsequent study, Loveys *et al.* (2003*a*) found no systematic differences in the degree of acclimation exhibited by mature leaves of the fast- and slow-growing species; it was speculated that the apparent contradiction between the two studies (Loveys *et al.*, 2002, 2003*a*) reflected the fact that Loveys *et al.* (2002) measured *R* rates in whole shoots (i.e. developing and mature leaves), whereas Loveys *et al.* (2003*a*) focused on the response of mature leaves only. If the degree of acclimation potential of developing leaves differs from that of mature leaves, then it may be that responses seen at the whole shoot level will differ from that of mature leaves alone. To date, no published studies have assessed the extent to which growth temperature affects rates of *R* in developing and mature leaves.

Another factor that could contribute to the discrepancy between Loveys *et al.* (2002) and Loveys *et al.* (2003*a*) could be the impact of temperature on respiratory flux in species that differ inherently in rates of respiration. Fast-growing species typically respire at a higher rate than their slow-growing counterparts (Poorter *et al.*, 1991; Atkin *et al.*, 1996; Loveys *et al.*, 2003*a*). In the absence of acclimation and assuming equal Q_{10} values in fast- and slow-growing species (Loveys *et al.*, 2003*a*), exposure to a new growth temperature will have a greater absolute effect on respiration in the fast-growing species. Conversely, changes in growth temperature would have less effect on respiration in inherently slow-growing species.

Taken together, the above studies demonstrate that changes in growth temperature do alter the relationship between RGR and its underlying components in comparisons of contrasting species, that variations in NAR play a greater role in determining interspecific differences in RGR at low growth temperature, and, finally, that the greater role of NAR at lower growth temperatures is due to rates of whole-plant *R* being more homeostatic across growth temperatures in slow-growing species than their fast-growing counterparts. Greater homeostasis of whole plant *R* in the slow-growing species (compared with fast-growing species) may reflect interspecific differences in the ratio of mature and immature tissues, as well as differences in specific rates of *R* and subsequent temperature responses of *R*.

Case study: responses to growth temperature in PICs

Do the trends observed in Loveys *et al.* (2002) across all species (irrespective of phylogeny) also exist within PICs? Here, a reanalysis from a PIC perspective of the effect of temperature on relationships between RGR and its underlying components is given. Figure 8 shows correlated change graphs (Wright and Westoby, 1999) of dSLA and dNAR values plotted against dRGR values for each PIC. Values were calculated by subtracting the attribute value for the favourable habitat from that of the unfavourable environment within each PIC. Positively correlated change would cause a point to fall in either upper-left or lower-right quadrants. For clarity of presentation, data for plants grown at 23 °C have not been shown. The correlated divergence between SLA and RGR was more consistent at 28 °C than at 18 °C (Fig. 8A), as shown by seven out of seven points (at 28 °C) versus four out of seven (at 18 °C) points falling in the top-right/lower-left quadrants (Fig. 8A). Moreover, for a given divergence in RGR, divergences in SLA were greater at 28 °C than at 18 °C. For correlated divergence between NAR and RGR, six out of seven points fell in the top-right/lower-right quadrants (Fig. 8B), with divergence in NAR generally being greater (for a given divergence in RGR) at 18 °C than at 28 °C. Thus, the SLA versus RGR and NAR versus RGR trends observed in Loveys *et al.* (2002) across all species (irrespective of phylogeny) are held within PICs but also changes in growth temperature alter the roles that SLA and NAR play in determining variations in RGR. At high growth temperatures, variations in RGR are strongly correlated with variations in SLA, irrespective of phylogeny. However, this relationship is less consistent at lower growth temperatures, suggesting that divergences in

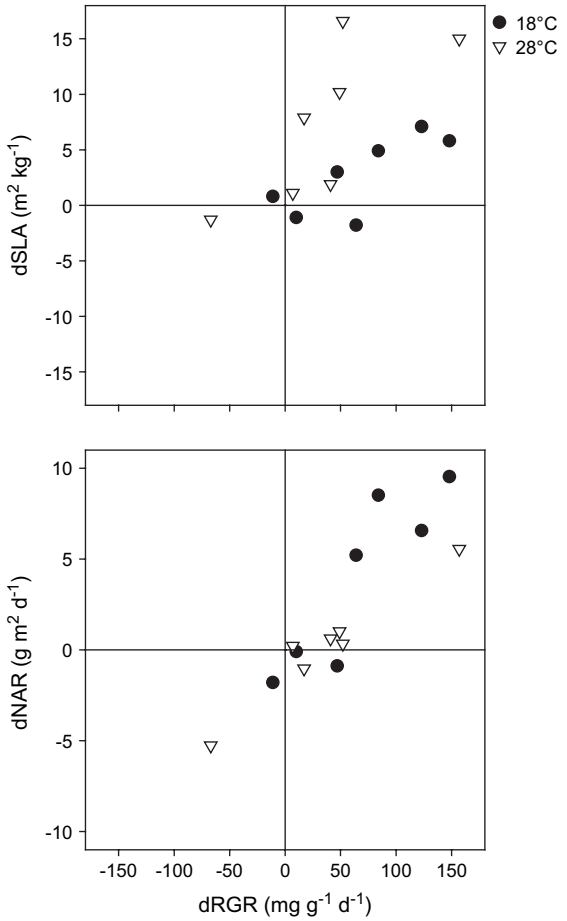

Fig. 8. Correlated-change graphs portraying divergences in (A) specific leaf area (dSLA, $m^2\ kg^{-1}$) and (B) net assimilation rate (dNAR, $g\ m^{-2}\ s^{-1}$), plotted against divergences in relative growth rate (dRGR, $g\ g^{-1}\ d^{-1}$) for plants grown at 18 °C (filled circles) and 28 °C (open triangles). Values were calculated by subtracting the attribute value for the favourable habitat from that of the unfavourable environment within each PIC. Positively correlated change would cause a point to fall in either upper-left or lower-right quadrants. For clarity of presentation, plants grown at 23 °C have not been shown. Data used to construct these graphs were taken from Loveys *et al.* (2003*b*).

leaf structure may become less important in determining divergences in growth rate as growth temperatures decrease. Conversely, NAR plays a greater role in determining RGR at lower growth temperatures. Such results cast some doubt on the generality of SLA being an important determinant of RGR of plants growing under cool field conditions and raise the prospect that divergences in NAR may play a greater role than previously thought in determining differences in RGR exhibited by closely related fast- and slow-growing species from contrasting environments.

Conclusions

In this review, how some plants, when challenged with contrasting growth temperatures, maintain relatively similar growth rates, is highlighted. Underpinning the response of RGR to growth is plasticity of a wide range of biochemical, anatomical, and morphological traits; collectively, such plastic responses contribute to homeostasis of metabolic activity, and potentially to maintenance of RGR in plants experiencing contrasting thermal regimes. Thus, acclimation of metabolism is intrinsically linked to plasticity of a range of biochemical and morphological traits. It has also been shown how plants often exhibit a trade-off between temperature-mediated changes in NAR and biomass allocation (in particular, changes in leaf structure that contribute to changes in SLA) when grown at different temperatures. The present analysis suggests that temperature-mediated changes in respiration play a pivotal role in determining NAR and thus RGR at different temperatures, particularly in plants grown at sub-saturating irradiance. It has also been shown that in comparisons that do not take phylogeny into account, fast-growing species exhibit greater temperature-dependent changes in RGR, SLA, and NAR than slow-growing plants (but with no systematic difference in the effect of temperature on biomass allocation between leaves, stems, and roots). Such trends are maintained with PICs for RGR and NAR [i.e. species adapted to more favourable habitats consistently exhibit greater temperature-mediated changes (and thus less homeostasis) in RGR and NAR than their congeneric counterparts adapted to less favourable habitats]. By contrast, no consistent trend in plasticity of SLA within PICs was found, suggesting that adaptation to contrasting habitats is not associated with systematic changes in plasticity of leaf structure. The present analysis has revealed the surprising fact that biomass allocation between leaves and roots is consistently more plastic in slow-growing species within each PIC. Finally, the review has highlighted how interspecific differences in plasticity/homeostasis alter the relationship between RGR and its underlying components, regardless of whether phylogeny is taken into account or not; it has been shown that variations in NAR account for an increasing proportion of variability in RGR as growth temperatures decrease. Conversely, the importance of SLA in determining interspecific variation in RGR could potentially increase if annual mean temperatures increase in the future.

Acknowledgements

This work was supported by grants from NERC in the UK (GR3/11898, NERC/A/S/2001/01186, NERC/B/S/2001/00875 to OKA), the Cooperative Research Centre for Greenhouse Accounting, Australia (BRL), the Nordic Academy of Advanced Studies (NorFA) Temperature Stress Network, and a Daphne Jackson Fellowship funded by the NERC (to LJA). We acknowledge the generous support provided by the Society for Experimental Biology and the *Journal of Experimental Botany* towards the running of the Plant Frontiers meeting in Sheffield.

References

Ackerly DD, Coleman JS, Morse SR, Bazzaz FA. 1992. CO_2 and temperature effects on leaf area production in two annual plant species. *Ecology* **73,** 1260–1269.

Armstrong AF, Logan DC, O'Toole P, Tobin AK, Atkin OK. 2005. Heterogeneity of plant mitochondrial responses underpinning respiratory acclimation to the cold in *Arabidopsis thaliana* leaves. *Plant, Cell and Environment* (in press).

Atkin OK, Botman B, Lambers H. 1996. The causes of inherently slow growth in alpine plants: an analysis based on the underlying carbon economies of alpine and lowland *Poa* species. *Functional Ecology* **10,** 698–707.

Atkin OK, Bruhn D, Hurry VM, Tjoelker MG. 2005*b.* The hot and the cold: unraveling the variable response of plant respiration to temperature. *Functional Plant Biology* **32,** 87–105.

Atkin OK, Evans JR, Ball MC, Lambers H, Pons TL. 2000*b.* Leaf respiration of snow gum in the light and dark: interactions between temperature and irradiance. *Plant Physiology* **122,** 915–923.

Atkin OK, Holly C, Ball MC. 2000*a.* 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.

Atkin OK, Scheurwater I, Pons TL. 2005*a*. High thermal acclimation potential of both photosynthesis and respiration in two lowland *Plantago* species in contrast to an alpine congeneric. *Global Change Biology* (in press).

Atkin OK, Tjoelker MG. 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science* **8,** 343–351.

Bednarz CW, van Iersel MW. 2001. Temperature response of whole-plant CO_2 exchange rates of four upland cotton cultivars differing in leaf shape and leaf pubescence. *Communications in Soil Science and Plant Analysis* **32,** 2485–2501.

Berry JA, Björkman O. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* **31,** 491–543.

Berry JA, Raison JK. 1981. Responses of macrophytes to temperature. In: Lange OL, Nobel PS, Osmond CB, Zeigler H, eds. *Physiological plant ecology.* I. *Responses to the physical environment.* Berlin: Springer-Verlag, 277–338.

Blackmann GE, Black JN, Kemp AW. 1955. Physiological and ecological studies in the analysis of plant environment. X. An analysis of the effects of seasonal variation in daylight and temperature on growth of *Helianthus annuus* in the vegetative phase. *Annals of Botany* **19,** 527–548.

Bloor JMG, Grubb PJ. 2004. Morphological plasticity of shade-tolerant tropical rainforest tree seedlings exposed to light changes. *Functional Ecology* **18,** 337–348.

Bradshaw AD. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* **13,** 115–155.

Bruhn D, Leverenz JW, Saxe H. 2000. Effects of tree size and temperature on relative growth rate and its components of *Fagus sylvatica* seedlings exposed to two partial pressures of atmospheric [CO_2]. *New Phytologist* **146,** 415–425.

Clarkson DT, Hopper MJ, Jones LHP. 1986. The effect of root temperatue on the uptake of nitrogen and the relative size of the root system in *Lolium perenne.* I. Solutions containing both NH_4^+ and NO_3^-. *Plant, Cell and Environment* **9,** 535–545.

Cunningham S, Read J. 2003. Comparison of temperate and tropical rainforest tree species: growth responses to temperature. *Journal of Biogeography* **30,** 143–153.

DeLucia EH, Heckathorn SA, Day TA. 1992. Effects of soil temperature on growth, biomass allocation and resource acquisition of *Andropogon gerandii* Vitman. *New Phytologist* **120,** 543–549.

Dewar RC, Medlyn BE, McMurtrie RE. 1999. Acclimation of the respiration/photosynthesis ratio to temperature: insights from a model. *Global Change Biology* **5,** 615–622.

Forward DF. 1960. Effect of temperature on respiration. In: Ruhland, W. ed. *Encyclopedia of plant physiology*, Vol. 12. Springer-Verlag, 234–258.

Friend AD, Woodward FI. 1990. Evolution and ecophysiological responses of mountain plants to the growing season environment. *Advances in Ecological Research* **20,** 59–124.

Garnier E, Freijsen AHJ. 1994. On ecological inference from laboratory experiments conducted under optimum conditions. In: Roy J, Garnier E, eds. *A whole plant perspective on carbon–nitrogen interactions.* The Hague: SPB Academic Publishing, 267–292.

Gifford RM. 1995. Whole plant respiration and photosynthesis of wheat under increased CO_2 concentration and temperature – long-term vs short-term distinctions for modelling. *Global Change Biology* **1,** 385–396.

Hendrickson L, Ball MC, Wood JT, Chow WS, Furbank RT. 2004. Low temperature effects on photosynthesis and growth of grapevine. *Plant, Cell and Environment* **27,** 795–809.

Hovenden MJ. 2001. The influence of temperature and genotype on the growth and stomatal morphology of southern beech, *Nothofagus cunninghamii* (Nothofagaceae). *Australian Journal of Botany* **49,** 427–434.

Hulme M. 1999. Air temperature in central England. In*:* Cannell MGR, Palutikof JP, Sparks TH, eds. *Indicators of climate change in the UK.* London: Department of Environment, Transport and Regions, 6–7.

Hurry VM, Druart N, Cavaco A, Gardeström P, Strand A. 2001. Photosynthesis at low temperatures. A case study with *Arabidopsis.* In: Li PH, Palva ET, eds. *Plant cold hardiness: gene regulation and genetic engineering.* New York: Kluwer Academic Press.

Hurry VM, Keerberg O, Pärnik T, Gardestrom P, Oquist G, Parnik T. 1995. Cold-hardening results in increased activity of enzymes involved in carbon metabolism in leaves of winter rye (*Secale cereale* L.). *Planta* **195,** 554–562.

Klikoff LG. 1966. Temperature dependence of the oxidative rates of mitochondria in *Danthonia intermedia*, *Penstemon davidsonii* and *Sitanion hystrix. Nature* **212,** 529–530.

Klikoff LG. 1968. Temperature dependence of mitochondrial oxidative rates of several plant species of the Sierra Nevada. *Botanical Gazette* **129,** 227–230.

Knight H, Zarka DG, Okamoto H, Thomashow MF, Knight MR. 2004. Abscisic acid induces CBF gene transcription and subsequent induction of cold-regulated genes via the CRT promoter element. *Plant Physiology* **135,** 1710–1717.

Körner C. 1999. *Alpine plant life. Functional plant ecology of high mountain ecosystems.* Berlin: Springer-Verlag.

Körner Ch, Larcher W. 1988. Plant life in cold environments. In: Long SF, Woodward FI, eds. *Plants and temperature.* Symposium of the Society for Experimental Biologists, Vol. 42. Cambridge: The Company of Biologists Limited, 25–57.

Kummerrow J, Ellis BA. 1984. Temperature effect on biomass production and root/shoot biomass ratios in two arctic sedges under controlled environmental conditions. *Canadian Journal of Botany* **62,** 2150–2153.

Kurimoto K, Day DA, Lambers H, Noguchi K. 2004*a.* Effect of respiratory homeostasis on plant growth in cultivars of wheat and rice. *Plant, Cell and Environment* **27,** 853–862.

Kurimoto K, Millar AH, Lambers H, Day DA, Noguchi K. 2004*b.* Maintenance of growth rate at low temperature in rice and wheat cultivars with a high degree of respiratory homeostasis is

associated with a high efficiency of respiratory ATP production. *Plant and Cell Physiology* **45,** 1015–1022.

Lambers H, Chapin FS, Pons TL. 1998. *Plant physiological ecology.* Springer-Verlag, New York.

Lambers H, Poorter H. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research* **23,** 187–261.

Larcher W. 2004. *Physiological plant ecology. Ecophysiology and stress physiology of functional groups.* Berlin: Springer-Verlag.

Larigauderie A, Körner Ch. 1995. Acclimation of leaf dark respiration to temperature in alpine and lowland plant species. *Annals of Botany* **76,** 245–252.

Long SP, Hutchin PR. 1991. Primary production in grasslands and coniferous forests with climate change – an overview. *Ecological Applications* **1,** 139–156.

Loveys BR, Atkinson LJ, Sherlock DJ, Roberts RL, Fitter AH, Atkin OK. 2003*a.* Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast- and slow-growing plant species. *Global Change Biology* **9,** 895–910.

Loveys BR, Scheurwater I, Pons TL, Fitter AH, Atkin OK. 2002. Growth temperature influences the underlying components of relative growth rate: an investigation using inherently fast- and slow-growing plant species. *Plant, Cell and Environment* **25,** 975–987.

Loveys BR, Scheurwater I, Pons TL, Fitter AH, Atkin OK. 2003*b.* Corrigendum. Growth temperature influences the underlying components of relative growth rate: an investigation using inherently fast- and slow-growing plant species. *Plant, Cell and Environment* **25,** 975–988. *Plant, Cell and Environment* **26,** 1927.

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.

Piersma T, Drent J. 2003. Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology and Evolution* **18,** 228–233.

Pisek A, Larcher W, Vegis A, Napp-Zinn K. 1973. *The normal temperature range.* In: Precht H, Christophersen J, Hensel H, Larcher W. *Temperature and life.* Berlin: Springer-Verlag, 102–194.

Poorter H, De Jong R. 1999. A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytologist* **143,** 163–176.

Poorter H, Garnier E. 1999. Ecological significance of inherent variation relative growth rate and its components. In: Pugnaire FI, Valladares F, eds. *Handbook of functional plant ecology.* New York, NY: Marcel Dekker, 81–120.

Poorter H, Van Der Werf A, Atkin OK, Lambers H. 1991. Respiratory energy requirements of roots vary with the potential growth rate of a species. *Physiologia Plantarum* **83,** 469–475.

Potter JR, Jones JW. 1977. Leaf area partitioning as an important factor in growth. *Plant Physiology* **59,** 10–14.

Ribas Carbó M, Aroca R, Gonzàlez Meler MA, Irigoyen JJ, Sanchez-Diaz M. 2000. The electron partitioning between the cytochrome and alternative respiratory pathways during chilling recovery in two cultivars of maize differing in chilling sensitivity. *Plant Physiology* **122,** 199–204.

Ryan MG. 1995. Foliar maintenance respiration of subalpine and boreal trees and shrubs in relation to nitrogen content. *Plant, Cell and Environment* **18,** 765–772.

Ryser P, Eek L. 2000. Consequences of phenotypic plasticity vs. interspecific differences in leaf and root traits for acquisition of aboveground and belowground resources. *American Journal of Botany* **87,** 402–411.

Schimel DS, House JI, Hibbard KA, *et al.* 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* **414,** 169–172.

Shipley B. 2000. Plasticity in relative growth rate and its components following a change in irradiance. *Plant, Cell and Environment* **23,** 1207–1216.

Stirling C, Heddell-Cowie M, Jones M, Ashenden T, Sparks T. 1998. Effects of elevated CO_2 and temperature on growth and allometry of five native fast-growing annual species. *New Phytologist* **140,** 343–354.

Stitt M, Hurry V. 2002. A plant for all seasons: alterations in photosynthetic carbon metabolism during cold acclimation in Arabidopsis. *Current Opinion in Plant Biology* **5,** 199–206.

Storkey J. 2004. Modelling seedling growth rates of 18 temperate arable weed species as a function of the environment and plant traits. *Annals of Botany* **93,** 681–689.

Strand A, Hurry V, Gustafsson P, Gardestrom P. 1997. Development of *Arabidopsis thaliana* leaves at low temperatures releases the suppression of photosynthesis and photosynthetic gene expression despite the accumulation of soluble carbohydrates. *The Plant Journal* **12,** 605–614.

Strand Å, Hurry V, Henkes S, Huner N, Gustafsson P, Gardeström P, Stitt M. 1999. Acclimation of Arabidopsis leaves developing at low temperatures: increasing cytoplasmic volume accompanies increased activities of enzymes in the Calvin cycle and in the sucrose-biosynthesis pathway. *Plant Physiology* **119,** 1387–1397.

Strand JA, Weisner SEB. 2004. Phenotypic plasticity: contrasting species-specific traits induced by identical environmental constraints. *New Phytologist* **163,** 449–451.

Talts P, Parnik T, Gardestrom P, Keerberg O. 2004. Respiratory acclimation in *Arabidopsis thaliana* leaves at low temperature. *Journal of Plant Physiology* **161,** 573–579.

Thomashow MF. 2001. So what's new in the field of plant cold acclimation? Lots! *Plant Physiology* **125,** 89–93.

Tjoelker MG, Oleksyn J, Reich PB. 1998*a.* Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO_2 and temperature. *Tree Physiology* **18,** 715–726.

Tjoelker MG, Oleksyn J, Reich PB. 1998*b.* Temperature and ontogeny mediate growth response to elevated CO_2 in seedlings of five boreal tree species. *New Phytologist* **140,** 197–210.

Tjoelker MG, Oleksyn J, Reich PB. 1999*a.* Acclimation of respiration to temperature and CO_2 in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biology* **5,** 679–691.

Tjoelker MG, Reich PB, Oleksyn J. 1999*b.* Changes in leaf nitrogen and carbohydrates underlie temperature and CO_2 acclimation of dark respiration in five boreal tree species. *Plant, Cell and Environment* **22,** 767–778.

Weih M, Karlsson PS. 2001. Growth response of mountain birch to air and soil temperature: is increasing leaf-nitrogen content an acclimation to lower air temperature? *New Phytologist* **150,** 147–155.

Westoby M. 2002. Choosing species to study. *Trends in Ecology and Evolution* **17,** 587.

Westoby M, Cunningham SA, Fonseca CR, Overton J, Wright IJ. 1998. Phylogeny and variation in light capture area deployed per unit investment in leaves: designs for selecting study species with a view to generalising. In: Lambers H, Poorter H, Van Vuuren MMI, eds. *Inherent variation in plant growth: physiological mechanisms and ecological consquences.* Leiden: Backhuys Publishers, 539–566.

Williams DG, Black RA. 1993. Phenotypic variation in contrasting temperature environments – growth and photosynthesis

in *Pennisetum setaceum* from different altitudes on Hawaii. *Functional Ecology* **7,** 623–633.

Woodward FI. 1979*a.* The differential temperature responses of the growth of certain plant species from different altitudes. I. Growth analysis of *Phleum alpinum* L, *P. bertolonii* D.C, *Sesleria albicans* Kit. and *Dactylis glomerata* L. *New Phytologist* **82,** 385–395.

Woodward FI. 1979*b.* The differential temperature responses of the growth of certain plant species from different altitudes. II. Analyses of the control and morphology of leaf extension and specific leaf area of *Phleum bertolonii* D.C. and *P. alpinum* L. *New Phytologist* **82,** 397–405.

Wright IJ, Westoby M. 1999. Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology* **87,** 85–97.

Xiong FS, Mueller EC, Day TA. 2000. Photosynthetic and respiratory acclimation and growth response of Antarctic vascular plants to contrasting temperature regimes. *American Journal of Botany* **87,** 700–710.

Zarka DG, Vogel JT, Cook D, Thomashow MF. 2003. Cold induction of *Arabidopsis* CBF genes involves multiple ICE inducer of CBF expression promoter elements and a cold-regulatory circuit that is desensitized by low temperature. *Plant Physiology* **133,** 910–918.

Ziska LH, Bunce JA. 1998. The influence of increasing growth temperature and CO_2 concentration on the ratio of respiration to photosynthesis in soybean seedlings. *Global Change Biology* **4,** 637–643.