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The relative importance of photosynthesis and respiration in determining growth rate

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Introduction

Global climate change is resulting in increases in the concentration of atmospheric CO_2 as well as changes in the daily, seasonal and annual mean temperatures experienced by plants. As most plant processes are temperature sensitive (Kramer and Kozlowski 1979) changes in temperature can have markedly different effects on the underlying physiological and biomass allocation parameters that contribute to plant growth. The relative growth rate (RGR) of plants adapted to resource-limiting habitats is often lower than their counterparts from resource-rich environments when grown under identical controlled conditions in the presence of adequate water and nutrients (Grime and Hunt 1975).

For many plant species, specific leaf area (SLA) is considered very important in determining RGR. However, net assimilation rate (NAR) is more closely correlated with changes in RGR in some studies (Pons 1977; Veenendaal *et al*. 1996). The effects of temperature on plant growth are likely to be partly mediated via its effect on photosynthesis and respiration and ultimately NAR. NAR is the end result of photosynthetic carbon gain and respiratory carbon release in respiratory processes (Lambers and Poorter 1992). Respiration and photosynthesis are both sensitive to short-term changes in temperature (Atkin *et al.* 2000a). However, the impact of long-term temperature changes on respiration and photosynthesis depends on the degree of thermal acclimation exhibited by these processes.

Acclimation can result in homeostasis of photosynthesis and/or respiration in plants grown at contrasting growth temperatures, when measured at their respective growth temperatures (Larigauderie and Körner 1995). Acclimation can occur in periods as short as several days (Tjoelker *et al*. 1999a; Atkin *et al*. 2000b). While some species exhibit little or no acclimation (Tjoelker *et al.* 1999b).

It has been shown that slow growing plant species respire a greater proportion of their acquired carbon than fast growing species (Poorter *et al*. 1990; Atkin *et al*. 1996a) when plants are grown at 20 ^{o}C. Changes in temperature may have markedly different effects on the efficiency of respiratory energy production/use in fast- and slow-growing species. Moreover, it is not known, whether fast- and slow-growing species differ systematically in the extent to which photosynthesis and/or respiration acclimates. In this paper we will examine the relative importance of acclimation of photosynthesis and respiration for affecting plant growth rate at different growth temperatures.

Materials and Methods

Plant material

Several fast and slow growing plant species with a range of growth forms were chosen. The species included; grasses- *Poa trivialis* L*., P. costiniana* J Vickery.; Forbs-*Achellia millefolium* L*., A. ptarmica* L*., Luzula acutifolia* Nordenskiold*., Geum rivale* Linn*., G. urbanum* L*., Plantago lanceolata* L*., P. major* L*., P. euryphylla* BG Briggs*., Silene dioica* L*.*, and *S. uniflora* Roth.; Shurbs- *Acacia melanoxylon* R.Br. and *A. aneura* F. Muell Ex Benth.; Trees- *Eucalyptus delegatensis* R. Baker. and *E. dumosa* Cunn. Ex. Schauer. After germination on John Innes No.2 compost the seedlings were transferred to 16 L hydroponics tanks filled with a fully aerated modified Hoagland's nutrient solution (pH 5.8) (Poorter and Remkes 1990). The tanks were placed in growth cabinets (Conviron E15, Winnipeg, Canada) with a 14 hour day, 300 μmol m^{-2} s^{-1} PPFD provided by a combination of 400 W metal halide and 400 W high pressure sodium blubs. The temperature treatments were constant 18, 23 and 28 ^{o}C.

Gas exchange

Whole plant gas exchange was measured on six of the 16 species used in the growth analysis; *S. uniflora, S. dioica, A. aneura, A. melanoxylon, P. costiniana* and *P. trivialis.* Whole shoot photosynthesis and dark respiration and root respiration were measured in four randomly selected plants of each species at each growth temperature (18, 23 and 28 ^{o}C). Intact plants were placed into cuvettes with the roots and shoots in separate compartments. The root compartment was filled with 1 L of nutrient solution as describe above with the addition of 10 mM MES. The solution was aerated during the course of the experiment. The irradiance and temperature was the same as that in the growth cabinets. CO_2 fluxes from the shoot and root compartments were measured using a Licor 6262 infra red gas analysis system (Licor, NE, USA) in an open system (Poorter and Welschen 1993).

Fresh and dry mass of leaves, stems and roots were determined. Tissues were freeze-dried in a Virtus, Unitop 600 SL freeze dryer (Gardiner, NY USA). Leaf area was determined using a LiCor, Inc 3100 leaf area meter (Lincoln, NE, USA).

Results

In most species, SLA increased as growth temperature increased (Fig 1a). At 18 ^{o}C the relationship between SLA and RGR was not significant ($P = 0.07$). At higher growth temperatures SLA became important in explaining differences in RGR; it explained 45% of the variation in RGR at 23 ^{o}C and 62% at 28 ^{o}C (Fig. 1a). NAR was positively correlated with RGR at all growth temperatures ($P < 0.0001$ at 18 ^{o}C; $P = 0.0021$ at 23 ^{o}C and $P < 0.0001$ at 28 ^{o}C). The extent to which variations in NAR were associated with variations in RGR was lowest at 23 ^{o}C, explaining only 48% of the variability while at 18 ^{o}C and 28 ^{o}C NAR explained 71% and 67% of the variation in RGR respectively (Fig 1b).

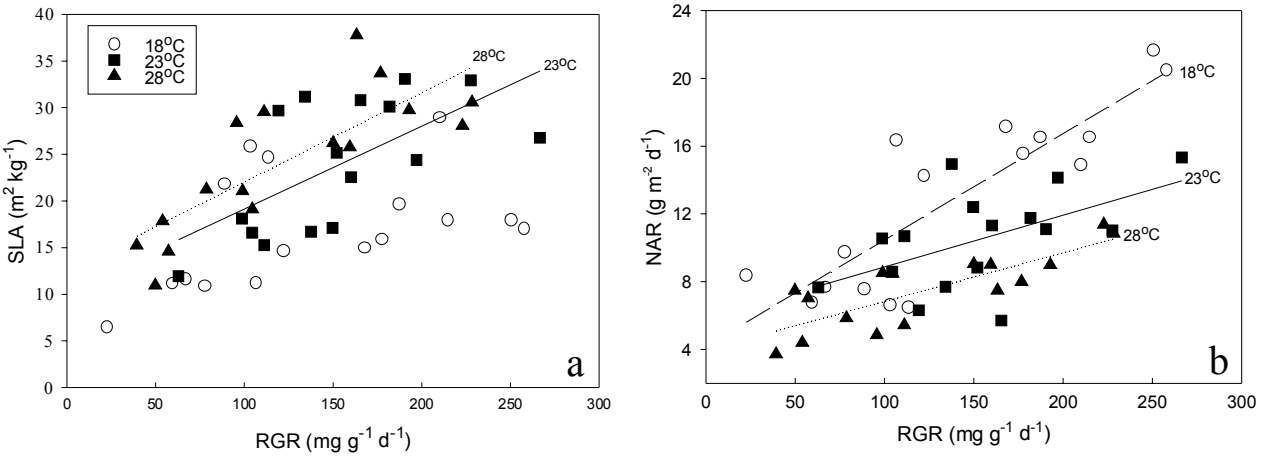

Figure 1. Components of relative growth rate at all three growth temperatures. (a) Specific leaf area, and (b) Net assimilation rate. Each value is the mean of 18-24 plants sampled over four harvests. Linear regressions are shown where significant.

There was no relationship between RGR and photosynthesis on an area basis (P_a) and no consistent change in P_a when plants were grown at different temperatures (Fig. 2a). Whole plant respiration (root plus shoot) expressed on a leaf area basis (R_a) per day was negatively correlated with RGR at all three growth temperatures (Fig 2b). The proportional change in whole plant daily respiration is shown in Figure 2c and shows that exposure to the lower temperatures had a greater inhibitory effect on R_a in the fast-growing species than in the slow-growing species.

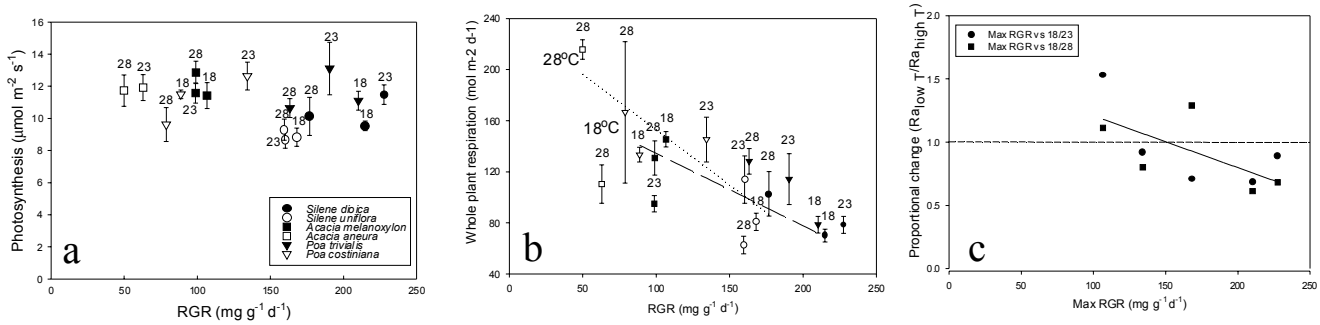

Figure 2. Variations in CO_2 exchange in six selected species. (a) photosynthesis on an area basis, (b) whole-plant respiration on a leaf area basis per day, (c) proportional change in respiration between growth temperatures. Each point is the mean of four replicates, SEM is shown. Linear regressions are shown where significant.

Figure 3 shows that there was a negative correlation between R/P and RGR, which was significant only in the case of the 18 ^{o}C treatment (P = 0.027, r^2 = 0.84). For plants grown at 28 ^{o}C the correlation was strong but not significant and the slope close to that for the 18 ^{o}C

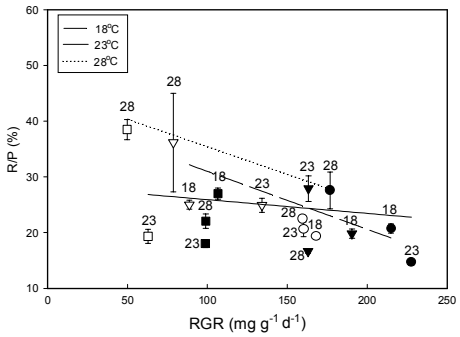

Figure 3. The ratio of photosynthesis to respiration for six selected species (symbols as in Fig. 2) grown at three temperatures. Linear regressions shown. Each point is the mean of four replicates, SEM is shown.

plants. For plant grown at 23 ^{o}C the relationship between RGR and R/P was almost flat with a slope of –0.02.

Discussion

Our results suggest that the association between RGR and NAR is important, and that between RGR and SLA negligible at lower growth temperatures compared to warmer growth temperatures. The results also suggest that the strong relationship between NAR and RGR at lower growth temperatures is due to inter-specific differences in the degree of respiratory acclimation.

A positive relationship between SLA and RGR was maintained when plants were grown at 23 and 28 ^{o}C. However, the correlation between SLA and RGR was not significant at 18 ^{o}C. This finding suggests that the commonly held view that SLA is the most important variable in determining variations in RGR is not necessarily true of plants experiencing cool growth temperatures. The lack of a significant relationship between SLA and RGR when plants were grown at 18 ^{o}C is likely to be due to variations in NAR largely determining differences in plant growth rates at cooler temperatures (Fig 1b). Figure 2a demonstrates that the higher NAR values exhibited by the 18 ^{o}C grown plants were not due to higher rates of P_a. Our data show that there was no correlation between whole shoot P_a and RGR, as reported previously (Poorter *et al.*1990). Moreover, our data demonstrate that the lack of correlation between P_a and RGR occurred at all three growth temperatures, with growth temperature not having a significant effect on P_a (Fig, 2a). Growth at the lower temperature must have suppressed carbon loss via respiration to a greater extent in the fast-growing species than in the slow-growing species. This can be seen clearly in Fig 2c where the proportional change in respiration between cool and warm growth temperatures is greater in the slow growing plants.

It is often assumed that as respiration is more temperature sensitive in the short term than photosynthesis, the R/P ratio will increase under growth conditions of elevated temperature (Woodwell 1990). However, such assumptions are rarely based on actual experimental data.

Gifford (1994) found that when a diverse range of species was grown at constant temperatures ranging from 15-30 ^{o}C, R/P remained constant. In contrast, our results demonstrate that R/P is sensitive to changes in growth temperature (being greater at 28 ^{o}C than at 18 ^{o}C in five of the six species measured) with the effect of temperature on R/P being greatest in the slow-growing species (Fig. 3). The percentage increase in R/P from 18-28 ^{o}C ranged from 36% for *S. dioica* to 66% for *P. trivialis*. The increase in R/P at 28 ^{o}C could result either from an increase in whole plant respiration rates and/or a decrease in the rate of whole shoot photosynthesis. The constancy of photosynthetic rates among the growth temperatures (Fig. 2a) demonstrates that increases in respiration (Fig. 3c) were responsible. This suggests that R_a did not fully acclimate (i.e. not homeostatic) to the high growth temperature.

In conclusion, we have shown that growth temperature can change the importance of the underlying components of RGR. Importantly, we have challenged the commonly accepted view that SLA is the most important factor driving RGR; our study shows that this does not necessarily apply at lower growth temperatures as there was no relationship between SLA and RGR at 18 ^{o}C. The importance of NAR at cool growth temperatures was due to differing degrees of acclimation of respiration across the range of RGR values. The proportion of photosynthesis respired was higher at 28 ^{o}C than at 18 ^{o}C.

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