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Altering root temperature does not directly effect photosynthetic rates in a temperate grassland community

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Introduction

Predictions from climate models have indicated that the global mean temperature is likely to rise by 1-4 °C during this century. Soil temperatures are likely to reflect changes in air temperature, although any change in cloudiness could complicate this. Warmer soil temperatures could potentially alter root growth (Kaspar and Bland, 1992), root respiration (Boone *et al.*, 1998) and nutrient uptake (Tindall *et al.*, 1990), with consequent effects on shoot physiology, specifically carbon acquisition.

Soybean (*Glycine max*) exposed to an increase in root zone temperature has been shown to increase photosynthetic rates (Ziska, 1998). The opposite has been found in bentgrass (*Agrostis palustris*) exposed to high soil temperatures (Xu & Huang, 2000) and no photosynthetic response of radish (*Raphanus sativus*) to a 5 °C increase in root zone temperature was observed (Kleier *et al.*, 2001). However, these experiments were performed in controlled environment chambers with a constant nutrient supply and the observed responses may not be reflected in a natural environment due to other environmental constraints. Moreover, these results demonstrate that the assimilatory response to root temperature is not consistent. The thermal origin of the species studied is likely to contribute significantly to the temperature response of that species and may explain some of this variability. Consequently it is important not only to use soil temperatures within the range that a species does, or is likely to, experience, but also to consider the daily and seasonal variations in those temperatures.

This paper describes the use of a soil warming system in a semi-natural ecosystem to increase the root zone temperature of a plant community. The system closely followed the ambient temperature, thus maintaining any environmental variation in soil temperature. Photosynthetic characteristics of two species in the system were measured along with the root responses of the whole plant community.

Materials and methods

Soil warming and shading: The soil warming system was set up on a bare soil site within the University of York Experimental Garden. Heating was provided by means of 1 x 0.5 m steel wire mesh grids, with a mesh size of 2 x 2 cm, which were pinned to the soil surface. Soil heating cable was tightly attached to the mesh allowing the heat to be spread more evenly than would be possible by heating cable alone. Soil temperatures were controlled using custom built controllers, which used six soil temperature probes, at 2 cm depth, in heated (3 probes) and ambient (3 probes) plots to adjust the heat input to the system.

The set-up followed a split plot design with 12 plots each consisting of 'heated' and 'ambient' sub-plots. A mesh was used in all 24 sub-plots irrespective of whether the soil was to be warmed. Shading was provided by means of a 1m high shade frame over each of the 12 plots. Soil temperature and moisture, air temperature and humidity, wind speed, PAR, and rainfall were all logged at 30 min. intervals using a DL2e logger (Delta-T Instruments, Cambridge, UK).

Plant Material: After the soil warming and monitoring systems were completed, in August 1998, the site was seeded with a mixture of temperate northern grassland species. The mixture consisted of: *Agrostis capillaries* (12%), *Cynosurus cristatus* (45%), *Festuca rubra* (25%), *Holcus lanatus* (5%), *Plantago lanceolata* (5%) and *Trifolium repens* (7%). The site was initially dominated by *P. lanceolata* but once occasional cutting was implemented *H. lanatus* became the dominant species. No attempt was made to control the species composition after seeding.

Experimental: The soil temperature of the heated plots was maintained at 3 °C above ambient. Shading was maintained at 2 levels, 85 and 60%, measured at a height of 70 cm above the soil surface. The soil temperature of 'ambient' shaded plots was maintained at that of 'ambient' non-shaded plots. Shading and soil warming were imposed on 2/2/2000 and were maintained for the duration of the experiment. Photosynthetic rates at saturating light levels ($1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) were measured on single *H. lanatus* and *P. lanceolata* leaves from each plot using a LiCor 6400 portable IRGA (Glen Spectra Ltd, Stanmore, UK) on 7/4/00, 12/5/00, 15/7/00, 25/8/00 and 29/9/00. Measurements of light and CO₂ response curves were made on *H. lanatus* leaves on 17 and 18/7/00. All the leaves used were subsequently harvested and the segment used for photosynthetic measurements cut out. Leaf area, fresh weight and dry weight of this segment were all determined. Root growth was estimated using 20 cm depth soil cores. Roots were extracted from the core by rinsing with cold water; forceps were used to remove soil particles still adhering to the roots. Root respiration was measured using oxygen electrodes (Hansatech Instruments, Kings Lynn, UK) and root dry weight was then determined.

Data Analysis: CO₂ curves were used to estimate respiration during daylight (R_d), electron transport capacity (J_{max}) and RubisCO activity ($V_{\text{c max}}$). Treatment effects on all measured parameters were determined using analysis of variance, provided by the GLM function of SPSS v10 (SPSS Science, Woking, UK). Where no significant shade effects existed, shade samples were combined for graphical representation of the soil warming results.

Results

Photosynthesis at saturating light (A_{sat}) was not effected by the soil heating treatment on any of the measurement dates in either *H. lanatus* or *P. lanceolata* (Fig. 1). Furthermore, there was little variation in A_{sat} during the growing season in either species. Shading treatments also had no effect on A_{sat} measurements. Light response curves did not show any difference in the light saturation point of photosynthesis between treatments, nor in leaf dark respiratory rates (R_n) (Table 1).

Stomatal conductance and transpiration in both species were unaffected by soil warming or shading for most of the year, but did exhibit a shade response during the late season measurements (29/9/00). The two species responded differently with *H. lanatus* having a higher transpiration rate and stomatal conductance in shaded plants whilst *P. lanceolata* had higher rates in non-shaded plants (data not shown).

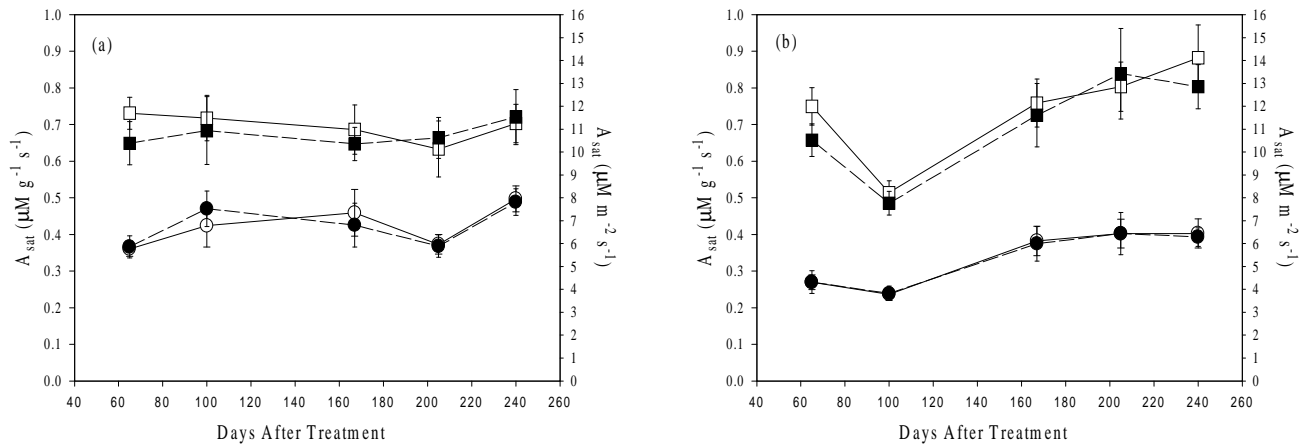


Fig. 1. Net photosynthesis at saturating light of (a) *Holcus lanatus* or (b) *Plantago lanceolata* plants grown at ambient (open symbols) or heated (closed symbols) soil temperatures, expressed on a dry weight (circles) or area (squares) basis.

Table 1. Leaf dark respiration rates and photosynthetic characteristics derived from CO₂ response curves. Different letters denote significant differences.

	R_n (nmol g ⁻¹ s ⁻¹)	R_d (nmol g ⁻¹ s ⁻¹)	$V_{c\ max}$	J_{max}
Ambient	26.7 ± 5.3 ^a	45.6 ± 8.5 ^a	1.11 ± 0.11 ^a	2.34 ± 0.05 ^a
Heated	15.1 ± 5.2 ^a	44.4 ± 8.0 ^a	1.06 ± 0.09 ^a	2.23 ± 0.12 ^a
Ambient/Full Shade	17.5 ± 5.0 ^a	42.5 ± 7.8 ^a	1.47 ± 0.19 ^b	3.07 ± 0.35 ^b
Heated/Full Shade	26.95 ± 5.1 ^a	44.5 ± 12.7 ^a	1.54 ± 0.1 ^b	2.95 ± 0.10 ^b

Soil heating also had no significant effect on the parameters derived from CO₂ response curves for *H. lanatus*. R_d , $V_{c\ max}$ and J_{max} were all unresponsive to the change in root temperature (Table 1). However, the shade treatments did have a significant effect on $V_{c\ max}$ and J_{max} , with both parameters increasing in response to shade. There was no interaction between this response and soil heating.

Root growth was estimated using root dry weigh and was reduced by soil warming (Fig. 2). Root dry weight varied throughout the year, increasing through spring and early summer then reducing during autumn and winter. Shading also caused a significant reduction in root dry weight, with shaded and heated plots having the lowest root dry weight by the final harvest. In contrast, root respiration was unaffected by soil temperature or shading (data not shown).

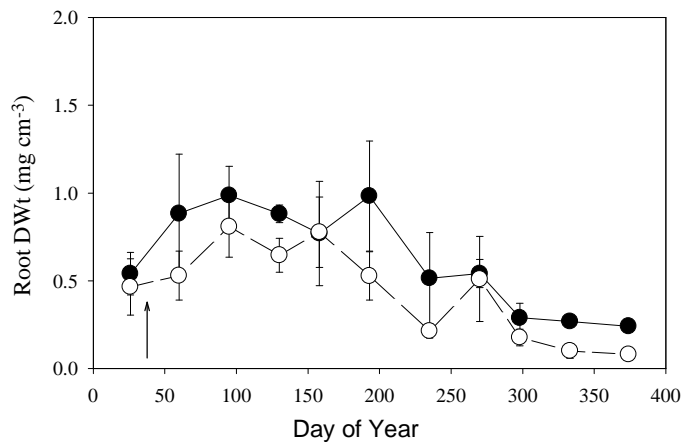


Fig. 2. Community root dry weight in heated (open symbols) and ambient (closed symbols) temperature soil. The arrow indicates the onset of soil warming.

Discussion

There are many ways in which roots may influence photosynthetic rates of plants. These include provision of water, nutrient uptake and assimilate use. It is commonly thought that root growth and respiration are largely determined by soil temperature (e.g. Drennan & Nobel, 1996). Consequently, it may be expected that changes in soil temperature may alter photosynthetic characteristics. Indeed, when root temperatures are severely reduced a reduction in transpiration and net photosynthesis due to reduced root water flow is seen (Wan *et al.*, 1999). However, there is ample evidence that when plants are studied in natural environments root growth is not limited by temperature, and that both root growth and respiration are well able to acclimate to seasonal changes in soil temperature (e.g. Fitter *et al.*, 1998). Conversely, it is likely that root growth is governed by received PAR via assimilate supply (Aguirrezabel *et al.*, 1994).

It may be expected from this that in a natural environment soil temperature would have little effect on photosynthetic rates, rather that changes in net photosynthesis may effect root growth. The results of the data presented here are consistent with this hypothesis. Not only was there no change in A_{sat} measurements with soil warming, but there was a reduction in root weight with shading. The other photosynthetic characteristics measured indicated that net photosynthesis at ambient light levels was also independent of soil temperature.

The 3 °C soil heating was enough to effect the plant community as evidenced by the reduction in root growth. However, it is not clear if this was a direct effect. The soil moisture data did not indicate any significant change in soil moisture status, so it is unlikely that drying soil lead to the reduction in root weight. It is possible that the increased soil temperature led to a change in mineralisation of nutrients, thereby altering their availability to the plants and thus allocation of assimilate to the root system.

Irrespective of whether heating effects on roots were direct or indirect there does not appear to have been any significant feedback to the photosynthetic machinery. Consequently, it appears that the plants acclimate to the potential effect of warmer soils on root water uptake. Furthermore, these data do not support the hypothesis that root growth will respond positively to global warming.

Acknowledgments

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