

Effects of soil temperature on growth, biomass allocation and resource acquisition of *Andropogon gerardii* Vitman

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SUMMARY

The effects of root temperature on growth and resource acquisition (carbon, nitrogen and phosphorus) were examined in *Andropogon gerardii*, a dominant C₄ grass of tallgrass prairies of the midcontinental USA. Soil temperature (5.9 to 35.5 °C) was manipulated independently from air temperature (c. 25/20 °C day/night) in a greenhouse. Total biomass at the end of the experiment and relative growth rate (RGR) were maximum at 25 °C soil temperature (T_{soil}) and decreased at higher and lower temperatures. T_{soil} had no effect on leaf area ratio (the ratio of leaf area to total biomass); thus the effect of T_{soil} on RGR was primarily through its influence on net assimilation rate (NAR). Different mechanisms may have contributed to decreases in NAR at sub- and supra-optimal T_{soil} . Soil temperatures below 20 °C caused significant reductions in foliar nitrogen (N) and phosphorus (P) concentration. High concentrations of these nutrients in roots suggest that nutrient transport was more strongly inhibited than uptake, and low foliar N and P may have contributed to reduced photosynthetic rates observed at 5 and 10 °C T_{soil} . Net photosynthesis was $< 12 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 5 and 10 °C T_{soil} and $> 20 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 15–40 °C. Changes in net photosynthesis did not therefore contribute to the reduction in NAR at supra-optimal T_{soil} . The strong growth dependence of *A. gerardii* on T_{soil} indicates that this abiotic factor may significantly limit productivity in tallgrass prairie, particularly early in the growing season.

Key words: *Andropogon gerardii*, nutrient uptake, photosynthesis, relative growth rate, soil temperature.

INTRODUCTION

Low soil temperature (T_{soil}) during the growing season may cause substantial reductions in the growth of plants in agronomic and native ecosystems, including tallgrass prairie. Although T_{soil} generally tracks air temperature, a number of situations may cause uncoupling of air and soil thermal regimes. The heat storage capacity of soil delays daily changes in T_{soil} relative to air temperature (Nobel & Geller, 1987). On longer time scales, a dense canopy of live or dead biomass can markedly delay seasonal increases in T_{soil} (Ehrenreich & Aikman, 1963; Hulbert, 1969; Old, 1969; Rice & Parenti, 1978). The accumulation of litter and standing dead biomass in unburned tallgrass prairie and the resulting depression of T_{soil} , particularly early in the growing season, has been implicated as an important factor reducing annual productivity (Old, 1969; Risser, 1985 and references therein; Knapp and Seastedt, 1986; Hulbert, 1988).

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The mechanisms of T_{soil} -induced reduction of growth are complex and may include direct effects on root growth and function, as well as indirect effects on shoot processes such as leaf expansion and net photosynthesis (A) (Cooper, 1973; Neilson, 1974). Low T_{soil} reduce root growth and nutrient uptake (Chapin, 1974; Bhat, 1982; Cumbus & Nye, 1985; Setter & Greenway, 1988; Tindall, Mills & Radcliffe, 1990; Pritchard *et al.*, 1990) and may also decrease root permeability and water uptake (Kramer, 1942; BassiriRad, Radin & Matsuda, 1991). Low stomatal conductance at low root temperature has been attributed to a decline in shoot water potential or other hydraulic or hormonal signals, and may result in stomatal limitations to carbon assimilation (Benzioni & Dunstone, 1988; Smith & Dale, 1988; Day, Heckathorn & DeLucia, 1991). Moreover, differences in the location of shoot meristematic tissue relative to the soil surface may contribute to different growth responses of grasses and herbaceous dicots to T_{soil} . The close proximity of leaf meristems to a cold substrate can result in direct inhibition of leaf expansion in grasses. Leaf expansion of maize seedlings is very sensitive to low

T_{soil} and this sensitivity is reduced by insulating the basal meristems near the chilled substrate (Watts, 1972; Engels & Marschner, 1990). Temperature of the elevated apical meristems of even a small herbaceous dicot or woody plant may, however, be independent of T_{soil} (DeLucia, Day & Oquist, 1991; Larigauderie *et al.*, 1991).

The objective of this study was to determine the effect of root temperature on growth of *Andropogon gerardii* Vitman, a dominant C_4 grass of tallgrass prairie. Hulbert (1988) reported that an increase in T_{soil} from 16.1 to 20.0 °C (10 cm depth) in the field caused a 34% increase in above-ground biomass and a 78% increase in the number of flowering stalks for *A. gerardii*. In this study T_{soil} (5.9–35.5 °C) was manipulated independently of air temperature (*c.* 25/20 °C day/night) under controlled conditions by inserting pots in temperature-controlled root boxes. Measurements of growth-analysis variables, nutrient uptake, leaf gas-exchange, and leaf water potential (ψ) were made to examine possible mechanisms of root-temperature control of plant growth.

MATERIALS AND METHODS

Plant material

Seeds of *Andropogon gerardii* Vitman collected at the Konza Prairie Research Natural Area (Manhattan, Kansas, USA; *c.* 39° 02' N latitude, and 96° 33' W longitude) were planted in a greenhouse in a mixture of vermiculite, ground peat, and loam soil (1:1:1, v/v) in 2 l pots. Several seeds were sown in each pot and plants were thinned to one per pot soon after emergence. Irradiance was supplemented with multi-vapour HID lamps (14 photoperiod), and photosynthetic photon flux density (PPFD, 400–700 nm) at pot height varied during the day from 700 to 2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$. Mean day and night air temperatures were 25 and 20 °C, respectively, and leaf temperature at midblade was within 3 °C of air temperature. Plants were watered daily and fertilized bi-weekly with a dilute N:P:K nutrient solution. Plants in all treatments remained vegetative for the duration of the experiment and, except for those at the temperature extremes, appeared vigorous.

Growth analysis

The effect of T_{soil} on growth and biomass allocation was determined by growth analysis as in Evans (1972) and Hunt (1990). After 25 d plants were sorted into 12 size classes and one plant from each size class was randomly assigned to nine treatments. One group was harvested immediately and served as the initial harvest for the remaining eight root-temperature treatments. The final harvest was done after 28 d under the treatment conditions. Plants were divided into blades, culms, and below-ground tissue (roots and rhizomes) and oven-dried at 70 °C

for 72 h. Prior to drying, leaf area (leaf = blade) was measured with a calibrated video area meter (Delta-T, Decagon, UK). Growth-analysis variables were calculated by two methods. In the first method relative growth rate (RGR) and net assimilation rate (NAR) were calculated using similarly ranked pairs of plants from the initial and final harvests. In the second method growth-analysis variables were calculated from the slope or product of slopes of linear regressions

$$\text{RGR} = \Delta \log_e W / \Delta t,$$

$$\text{NAR} = \Delta \log_e LA / \Delta t \times \Delta W / \Delta LA,$$

where W , t , and LA are dry mass, time, and leaf area, respectively. In this second method plant ranking did not influence the calculations. The differences in values calculated by the two methods was < 4% suggesting that plant size \times treatment interactions were minimal. The data presented in this paper are those calculated by the first method using ranked plants.

Temperature treatments

Root temperature was controlled by inserting pots through holes in the lids of thermostated root boxes (EGC, M49, Chagrin Fall, Ohio), and pots were insulated by placing foam insulation (3 cm thick) on the soil surface. The insulation did not cover the entire surface and permitted gas exchange from the soil. Target T_{soil} ranged from 5 to 40 °C in 5° increments. Actual T_{soil} were monitored continuously with copper-constantan thermocouples placed in the geometric centre of one pot per treatment. The thermocouples were sampled with a datalogger (Campbell CR-21X, Logan, UT, USA). Average T_{soil} for the duration of the experiment were: 5.9, 10.1, 15.2, 20.2, 24.5, 29.7, 33.9 and 35.5 °C. Temperature variation within each pot and treatment was generally ≤ 1.0 °C. Each root box was under an HID lamp and boxes were moved to different positions in the greenhouse every 3–4 d.

Gas exchange measurements

Immediately before the final harvest, gas-exchange and leaf water potential were measured on the midsection of recently expanded leaves from five plants per treatment. A (CO_2 flux) and transpiration were measured with an open-flow, infrared gas-analysis system (LCA-2, Analytical Development Co., UK). The CO_2 concentration of air entering the leaf cuvette was maintained at 350–360 $\text{cm}^{-3} \text{m}^{-3}$ by mixing compressed air and 1% (v/v) CO_2 in nitrogen. The cuvette (Parkinson Leaf Chamber, Analytical Development Co.) contained a capacitive humidity sensor and a high-speed fan to increase boundary layer conductance. The boundary layer conductance of a filter paper leaf replica was 0.83 mol

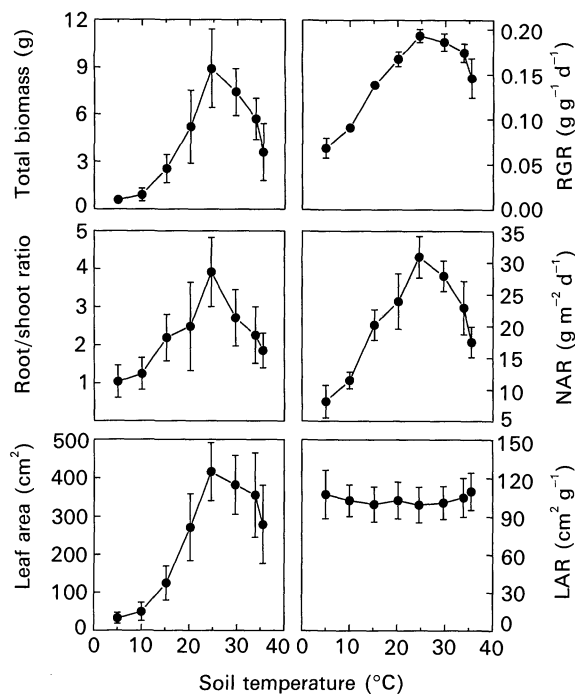


Figure 1. Biomass and growth-analysis parameters for *Andropogon gerardii* grown at target T_{soil} from 5 to 40 °C and *c.* 25/20 °C (day/night) air temperature. Actual mean T_{soil} were: 5.9, 10.1, 15.2, 20.2, 24.5, 29.7, 33.9, and 35.5 °C. The growth-analysis variables are: RGR, relative growth rate; NAR, net assimilation rate; LAR, leaf area ratio. These values were calculated over a defined growth interval. Each value is the mean of 12 plants (± 1 SD). T_{soil} had a significant effect ($P \leq 0.05$) on all dependent variables except LAR.

$\text{m}^{-2} \text{s}^{-1}$, and this value was used in the calculation of stomatal conductance. Leaf temperature was measured in the cuvette with a fine-wire copper-constantan thermocouple appressed to the abaxial leaf surface and was maintained at 25 ± 0.5 °C (range) by passing cooled air over the cuvette. Relative humidity in the cuvette was generated by transpiration and was 35–60% depending on the treatment. The reported ranges in leaf temperature and r.h. refer to values measured for different leaves. Each gas-exchange measurement was completed in 20–40 s and these variables were nearly constant over this time. A PPFD perpendicular to the leaf of $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ was provided by a multivapour HID lamp projected through 10 cm of water. A , stomatal conductance to water vapour (g , assuming negligible cuticular transpiration), and intercellular CO_2 concentration (c_i) were calculated as in von Caemmerer & Farquhar (1981). Leaf water potential was measured on an adjacent leaf with a pressure chamber (Soil Moisture Co., Santa Barbara, CA, USA).

Nitrogen and phosphorus determinations

Oven-dried root and shoot tissue was ground to 40 mesh in a Wiley mill and analysed for nitrogen (N)

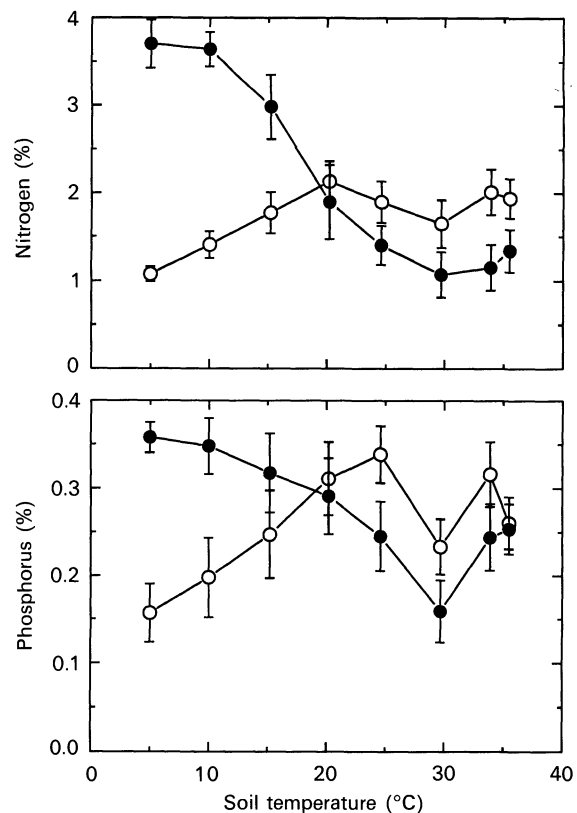


Figure 2. The effect of T_{soil} on root (●) and shoot (○) nitrogen and phosphorus concentration of *Andropogon gerardii*. Nutrient concentrations are expressed as a percentage of dry mass, and each value is a mean (± 1 SD) of 12 plants. T_{soil} had a significant effect ($P \leq 0.05$) on all dependent variables.

and phosphorus (P) concentration following Kjeldahl digestion (Lowther, 1980). Nitrogen concentration was determined using an ammonium analyser (model 360, Wescan Inst., Santa Clara, CA) and P was assayed colorimetrically (John, 1970). Phosphorus analyses were not performed on plants from the first harvest.

Statistical analyses

Means of the dependent variables were compared statistically with a one-way ANOVA and Tukey multiple-range test (STATISTIX, Analytical Software, MN, USA).

RESULTS

Total plant biomass and the other static growth variables, root/shoot ratio and leaf area, were affected strongly by different T_{soil} regimes; the optimum T_{soil} for biomass and these other variables of *A. gerardii* was 25 °C (Fig. 1). RGR and NAR also had a T_{soil} optimum of 25 °C. Leaf area ratio (LAR), however, was not affected by soil temperature (Fig. 1). Specific leaf area (SLA) increased from 0.0273 ± 0.0017 (SD) $\text{m}^2 \text{g}^{-1}$ at 5 °C T_{soil} to 0.0295 ± 0.0008 $\text{m}^2 \text{g}^{-1}$ at 26 °C ($P < 0.05$ one-way ANOVA, data not shown).

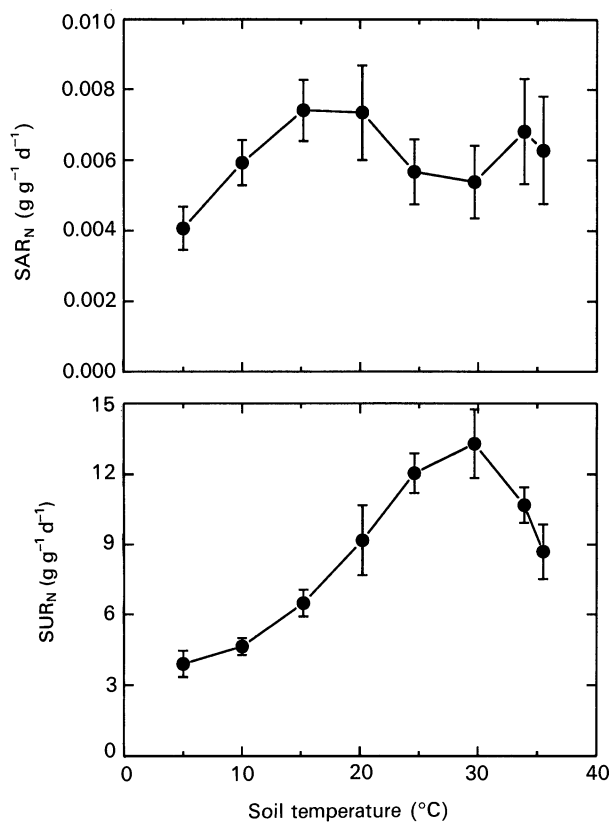


Figure 3. The effect of T_{soil} on mean specific absorption rate (SAR) and mean specific utilization rate (SUR) of *Andropogon gerardii*. Instantaneous SAR = $(1/R)(dM/dt)$, where R is root dry mass and M is total plant N. Instantaneous SUR = $(1/M)(dW/dt)$, where W is dry mass. SAR and SUR were calculated as mean values over the growth interval as in Hunt (1990). Each value is the mean (± 1 SD) of 12 plants. T_{soil} had a significant effect ($P \leq 0.05$) on SAR and SUR.

T_{soil} altered root and shoot N and P concentrations (Fig. 2). The high concentrations of N and P in roots and low concentrations in shoots at low soil temperatures suggests that cold soil may have inhibited transport of these nutrients above ground. In addition, low growth rates may have had a concentrating effect on N and P levels at low soil temperatures. With the possible exception of an aberrant point for P at 30 °C, shoot N and P increased as T_{soil} increased from 5 to 20 °C and remained relatively stable at higher T_{soil} . The inverse of this pattern was observed for root N and P – the concentration of these nutrients decreased with increasing T_{soil} until *c.* 20 °C (Fig. 2).

Specific absorption rate of nitrogen (SAR_N, g N g root⁻¹ d⁻¹) provides an index of the nitrogen uptake efficiency of roots (Hunt, 1990). Although low values of SAR_N at 25 and 30 °C T_{soil} render this variable difficult to interpret, it appears that SAR_N was inhibited by temperature only at 5 °C (Fig. 3). The effect of T_{soil} on the specific utilization rate for nitrogen (SUR_N, g total dry mass g N⁻¹ d⁻¹) was similar to the static biomass variables in Figure 1, except the temperature optimum occurred at 30 °C.

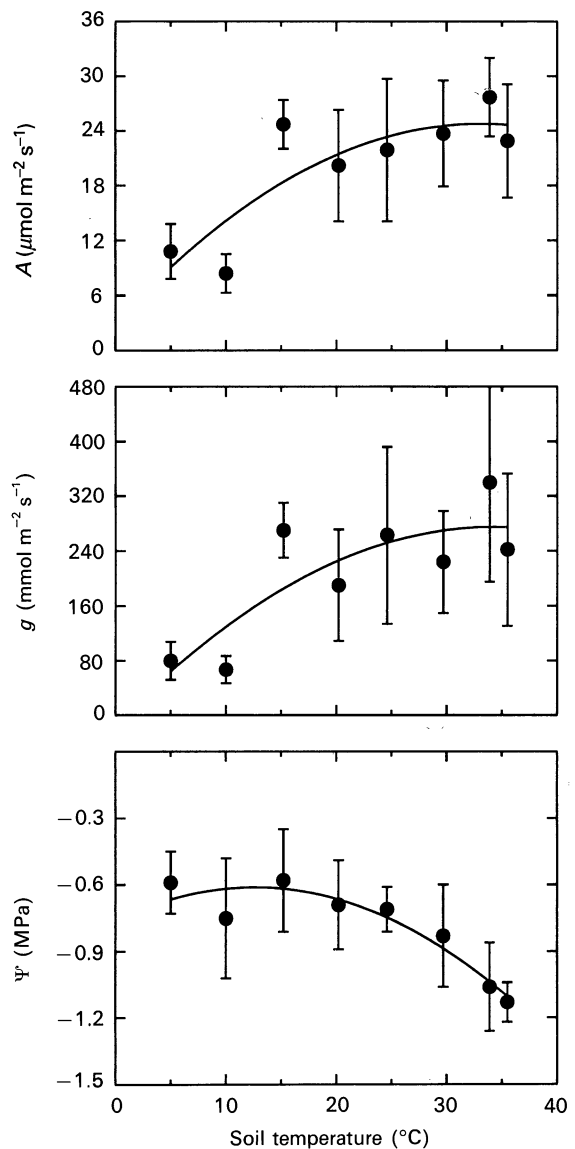


Figure 4. The effect of T_{soil} on net photosynthesis (A), stomatal conductance to water vapour (g), and leaf water potential (ψ) of *Andropogon gerardii*. Measurements were made at midday on 5 plants per treatment; means are ± 1 SD. T_{soil} had a significant effect ($P \leq 0.05$) on all dependent variables. Lines represent least-square polynomial regressions.

SUR_N is the rate of biomass accumulation per unit nitrogen and is an index of the efficiency of nitrogen utilization (Hunt, 1990). SAR and SUR were not calculated for P because tissue from the initial harvest inadvertently was not analysed for this element.

T_{soil} below 15 °C caused significant reductions of A and g (Fig. 4). Intracellular CO₂ concentration (c_i) at 25 °C T_{soil} was 170 ± 50 cm³ m⁻³ (SD) and was not significantly affected ($P > 0.05$) by T_{soil} (data not shown). In contrast to the growth responses, the effect of T_{soil} on gas exchange was asymptotic and attained a maximum at T_{soil} of 15 °C. Low T_{soil} had no effect on ψ (Fig. 4). However, a decrease in ψ was evident at $T_{\text{soil}} > 30$ °C and was probably caused by higher transpiration rates at these temperatures.

DISCUSSION

Variation in T_{soil} at constant air temperature had a significant effect on growth rate, total biomass, and biomass allocation of *Andropogon gerardii*. With the exception of mean LAR, all growth variables had a distinct T_{soil} optimum of 25 °C. Different mechanisms may have operated to decrease growth above and below this optimum. Impaired nutrient translocation and reduced growth capacity of meristems may have been limiting at suboptimal T_{soil} , whereas increased root respiration may have been the dominant limitation at supra-optimal temperatures.

Several studies have reported a decrease in root/shoot ratio with increasing T_{soil} (Wilson, 1988; discussed in Larigauderie *et al.*, 1991). In an examination of 12 pasture species grown at the same air temperature, Davidson (1969) observed a decrease in root/shoot ratio with increasing root temperature from 5 °C to greater than 25 °C for all species. The root temperature at which the greatest leaf production occurred was species dependent – maximum leaf production occurred at a root temperature of 35 °C for subtropical species and at *c.* 20 °C for cool temperate species. Davidson (1969) postulated that root/shoot ratio should decrease with increasing T_{soil} because higher temperature would increase rates of root function. This is consistent with the predictions of Thornley's (1972) model of root/shoot allocation. An assumption of Davidson (1969) and Thornley (1972) is that the only effect of temperature on root/shoot ratio is through its influence on resource acquisition or partitioning. The increase in root/shoot ratio with increasing T_{soil} for *A. gerardii* (Fig. 1) suggests a direct low-temperature limitation of the growth capacity of root meristems or reductions in the extent of cell expansion (Pritchard *et al.*, 1990). Roots and rhizomes were not separated in this study and it is possible that a decrease in root/shoot ratio occurred with increasing temperature and was offset by a large increase in rhizome mass. However, an increase in root/shoot ratio with increasing T_{soil} has also been observed in *Phaseolus vulgaris* (Brouwer, 1964), maize (Grobbelaar, 1963), and *Ceanothus greggii* (Larigauderie *et al.*, 1991). Because root growth may be dependent on current photosynthate, inhibition of carbohydrate translocation from shoots to roots by low T_{soil} (Marowitch, Richter & Hoddinott, 1986) may also contribute to low root/shoot ratios in cold soil.

RGR is defined as the product of NAR and LAR (Evans, 1972; Hunt, 1990). This is, however, mathematically correct only for instantaneous values. Though not strictly multiplicative for mean values calculated over a growth interval, inferences regarding the relative contribution of NAR and LAR to changes in RGR are valid. Suboptimal T_{soil} caused a significant increase in NAR and had no

effect on LAR (Fig. 1). Because of the close proximity of leaf meristems to the soil, leaf expansion in grasses may be inhibited directly by heat loss to the substrate or to cold water in the transpiration stream (Setter & Greenway, 1988; Engels & Marschner, 1990). Leaf area of *A. gerardii* was substantially reduced at low T_{soil} ; however, the ratio of assimilatory surface area to plant biomass, indicated by the mean LAR, was unaffected. Despite lower SLA, the decrease in root/shoot ratio contributed to the maintenance of high LAR at suboptimal T_{soil} . Thus, the dominant effect of suboptimal T_{soil} on RGR appears to have been through inhibition of NAR.

NAR reflects total daily carbon gain per unit leaf area minus whole-plant respiration. T_{soil} below 15 °C significantly reduced A (Fig. 4) and NAR. Low T_{soil} reduces root hydraulic conductivity (Radin, 1990; BassiriRad *et al.*, 1991) and possibly the production of phytohormones (Belding & Young, 1989). In some cases these factors may contribute to reduced stomatal conductance and photosynthesis at low root temperature. For *A. gerardii*, however, intercellular CO_2 concentration was unchanged and ψ was relatively high at low T_{soil} , indicating that direct water-stress effects or endogenous root signals influencing stomatal aperture were not dominant limitations to photosynthesis at these low temperatures. Thus, non-stomatal factors may have reduced net photosynthesis at suboptimal T_{soil} . These non-stomatal factors may include carbohydrate feedback limitations (Herold, 1980; Sharkey & Vanderveer, 1990) or limitations by low foliar concentrations of nitrogen, phosphorus or other nutrients.

Nutrient uptake in a wide spectrum of plants is markedly temperature dependent and varies with the particular nutrient (Chapin, Van Cleve & Tryon, 1986; Setter & Greenway, 1988; Tindall *et al.*, 1990). For tomato, uptake of potassium and iron were most reduced at low root temperatures, followed by calcium, nitrate, zinc, and manganese (Tindall *et al.*, 1990). Low T_{soil} also caused significant reductions in the flux of potassium and nitrate ions through excised roots of *Hordeum vulgare* and *Sorghum bicolor* (BassiriRad *et al.*, 1991). In *A. gerardii* the specific absorption rate for nitrogen (SAR_N) at 5 °C was only slightly lower than at 25 or 30 °C (Fig. 3); however, translocation of nitrogen and phosphorus from roots to shoots may have been impaired (Fig. 2). High nitrogen concentrations in the roots and reduced growth at low root temperature caused a decrease in nitrogen-use efficiency expressed as the specific utilization rate for nitrogen (SUR_N) (Fig. 3). The temperature-induced reduction in translocation of N and P to shoots may have contributed to low rates of net photosynthesis at T_{soil} below 15 °C.

There were no significant differences in leaf gas-exchange, SAR_N , or tissue nutrient concentrations at

supra-optimal T_{soil} . The respiration rate of plant tissues approximately doubles with each 10 °C increase in temperature, and we postulate that increased T_{soil} from 25 to 35 °C may have increased the rate of root respiration and caused the decrease in NAR and thus decreased RGR at root temperatures above 25 °C.

In addition to increasing irradiance at the soil surface and nitrogen availability, the increase in T_{soil} resulting from the removal of litter by spring burning has been implicated as a factor increasing productivity of grasslands (see Introduction). In unburned grasslands soil temperatures at 10 cm depth do not reach the temperature optimum for growth of *A. gerardii* (25 °C) until late May in Oklahoma (Kelting, 1957; Adams & Anderson, 1978; Rice & Parenti, 1978) or even mid-June in Kansas (Hulbert, 1969). Vegetative growth of *A. gerardii* is initiated in early April (McKendrick, Owensby & Hyde, 1975). Thus, growth of this species may be limited by T_{soil} for a month or more early in the growing season. Removal of litter by fire can cause soils to warm to 25 °C a full month earlier. By mid-June T_{soil} may exceed 30 °C and be supra-optimal for growth of *A. gerardii*. High T_{soil} late in the season inhibit root growth at a time when soil moisture is low and may exacerbate water stress for prairie grasses.

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