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RAPID COMMUNICATION

Atmospheric vapor pressure deficit is critical in predicting growth response of "cool-season" grass *Festuca arundinacea* to temperature change

Thomas Sinclair · Edwin Fiscus · Ben Wherley · Michael Durham · Thomas Rufty

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Abstract There is a lack of information on plant response to multifactor environmental variability including the interactive response to temperature and atmospheric humidity. These two factors are almost always confounded because saturated vapor pressure increases exponentially with temperature, and vapor pressure deficit (VPD) could have a large impact on plant growth. In this study using climate controlled mini-greenhouses, we examined the interacting influence of temperature and VPD on long-term growth of tall fescue (*Festuca arundinacea* Schreb), a cool season grass. From past studies it was expected that growth of tall fescue would decline with warmer temperatures over the range of 18.5–27°C, but growth actually increased markedly with increasing temperature when VPD was held constant. In contrast, growth declined in experiments where tall fescue was exposed to increasing VPD and temperature was held constant at 21°C. The inhibited growth appears to be in response to a maximum transpiration rate that can be supported by the tall fescue plants. The sensitivity to VPD indicates that if VPD remains stable in future climates as it has in the past, growth of tall fescue could well be stimulated rather than decreased by global warming in temperate climate zones.

Keywords Growth · Tall fescue · Temperature · Transpiration · Vapor pressure deficit

Introduction

Plant growth is sensitive to the combination of variables defining the abiotic environment, however, there is little information available on plant response to multifactor environmental changes (Walthier et al. 2002). Shaw et al. (2002), for example, found that the net primary production of a grassland was quite different with the interacting components of climate change compared to that predicted from a single factor. One confounding factor that is often overlooked is vapor pressure deficit (VPD) of the atmosphere. Short-term studies have shown that VPD can have a direct effect on stomatal conductance and photosynthesis (Woledge et al. 1989), which could markedly alter plant response to other environmental changes. Surprisingly, there is virtually no information on plant growth when subjected to constant VPD levels over extended periods.

In the experiment we report here, the growth of the "cool-season" grass tall fescue was studied to examine its long-term growth response to the interactive influence of temperature and VPD. The common reference to tall fescue as a cool-season grass results from the observations of poor performance under sustained hot conditions (Duble 2004). Indeed, controlled-temperature experiments have found that growth is decreased above a day/night temperature of 21/16°C (Hill et al. 1985) and leaf photosynthetic rate was substantially decreased at 25°C as compared to 15°C (Woledge and Jewiss 1969). However, these previous experimental results did not consider variation in VPD resulting from the experiment treatments and were likely confounded by substantial increases in VPD that can be associated with increasing temperature.

T. Sinclair (✉)
Agronomy Department, University of Florida,
P.O. Box 0965, Gainesville, FL 32611-0965, USA
e-mail: trsincl@ifas.ufl.edu

E. Fiscus · B. Wherley · T. Rufty
Crop Science Department, North Carolina State University,
Raleigh, NC 27695-7620, USA

E. Fiscus · M. Durham
US Department Agriculture, Agricultural Research Service,
3908 Inwood Road, Raleigh, NC 27603, USA

Temperature and VPD are almost always confounded in experiments because saturated vapor pressure increases exponentially with increasing temperature. Hence, the difference between saturated vapor pressure and actual vapor pressure, i.e., VPD, can be greatly increased with increased-temperature treatments. Since plant water loss, i.e., transpiration, is directly proportional to VPD, water transport in the plant must increase in response to VPD. However, threshold VPD levels have been identified above which water transport in the plant can no longer match the transpirational demand. At that point, stomatal conductance decreases to stabilize transpiration at a constant, maximum rate (Bunce 1981; Turner et al. 1984) and decreased CO_2 diffusion limits photosynthesis. The threshold VPD in many species occurs in the range of 2.0–2.5 kPa (Turner et al. 1984; Fletcher et al. 2007). In one species, *Arbutus unedo* L., maximum transpiration rate was achieved at VPD as low as 1.0 kPa (Turner et al. 1984).

The objective of this study was to observe the growth of tall fescue in response to the interactive influence of temperature and VPD. The experiments were conducted in small, climate-controlled greenhouses, which allowed plants to be exposed to near natural light levels while being subjected to various constant levels of temperatures and VPD. The results from these 6 week experiments clearly indicated a major response in plant growth directly associated with VPD level.

Materials and methods

Plant material

Pots with a 12 l volume and a top surface area of approximately 570 cm^2 were filled with a light sandy loam soil mixed with a complete fertilizer. Cultivar 'Kentucky 31' tall fescue was sown into the pots and grown for a 10 week establishment period. In this period, a thick turf canopy developed resulting in virtually complete interception of incident solar radiation. Once the turf canopy was established, the complete fertilizer was again applied and the pots were moved into the mini-greenhouses. The grass was allowed to acclimate to the treatment conditions for 1 week and then the data collection began. The pots were irrigated each night to replace the water loss, and nutrient solution was added following the harvesting of tissue each week over a 6 week period.

Greenhouses

Four small (1.2 × 2.4 m) greenhouses, modified from those previously described (Fiscus et al. 1999), were used for the experiments. The center height of the greenhouses was increased from the original to 1.3 m in these experiments. Air circulation through the greenhouses resulted in three exchanges of chamber volume per minute. The environment in each chamber was under constant control to maintain preset values of temperature, humidity, and CO_2 in each greenhouse. A temperature/humidity sensor (model HMW71Y, Vaisala) was placed in each greenhouse to continuously monitor each environment. Carbon dioxide concentration was held constant during the daylight hours at 375 $\mu mol\ mol^{-1}$. Plants were exposed only to ambient light passing through the FEP teflon film covering the greenhouses (0.13 mm thick, E.I. DuPont Nemours), which transmitted 90% of daily solar radiation.

Water loss from the pots was measured continuously by weight changes of the pots. Two balances with 1 g resolution (Model I20-W, Ohaus Inc.) were placed in each greenhouse and two grass pots were placed on each balance. Weight on each balance was continuously averaged and recorded every 5 min. Since virtually no solar radiation reached the soil surface in these pots, these data were used to calculate weekly transpiration rates by summing the total weight loss after accounting for the weight changes due to irrigation and fertilization.

Grass growth was measured by clipping the shoots each week to a height of 7.5 cm. The clippings for each pot were collected, dried at 70°C, and weighed to determine weekly shoot growth. There was no trend in growth or water loss over the 6 weeks of measurements in each experiment so the growth and water loss rates during the experimental treatments was calculated as the means of the six weekly observations.

Environmental treatments

The environment in each greenhouse was held constant throughout the duration of the experiment. The first experiment was designed to measure plant growth under four constant temperature treatments (18.5, 21, 24, or 27°C) while holding the VPD constant in all greenhouses at 1.2 kPa. The second experiment was designed to measure the response of plant growth to VPD while holding a constant temperature. The VPD treatments obtained in the greenhouses were 0.9, 1.2, 1.4, or 1.7 kPa while temperature was held constant at 22°C in all greenhouses.

Results and discussion

Temperature treatments in the first experiment were selected to cover the range from reported optimum temperature to excessively high temperature for tall fescue. The expectation based on published studies (Hill et al. 1985; Woledge and Jewiss 1969) was that growth of tall fescue would be greater at the two lower temperatures, 18.5 and 21°C, while the two higher temperatures, 24 and 27°C, would be deleterious.

In direct contrast to the anticipated results, the weekly growth of the tall fescue was substantially increased with increased temperature (Fig. 1a). Growth at 24 and 27°C was about 2.3 times that at 18.5°C and 1.4 times that at 21°C. The VPD surrounding the plants was equal across the temperature treatments so that nearly equal transpiration rates were obtained across temperature treatments. Consequently, control of VPD at constant value across temperature treatments resulted in a growth response by tall fescue exactly opposite what was anticipated for this cool season species.

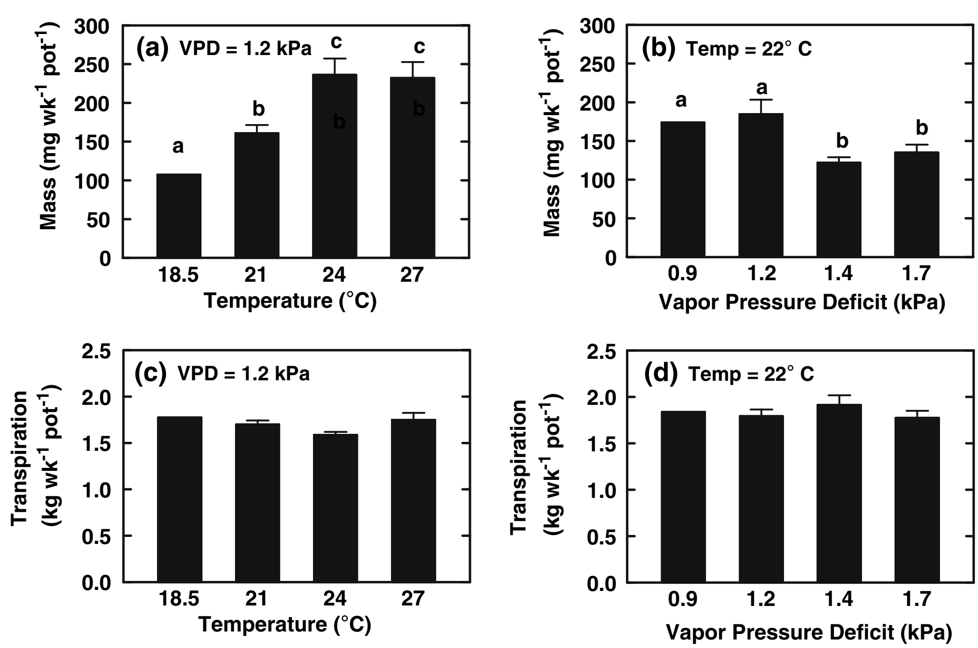
The VPD treatments in the second experiment were designed to evaluate whether VPD had an influence on growth even when plants were grown at an apparent optimal temperature. There was a strong, negative influence of increasing VPD on plant growth (Fig. 1b). Maximum growth was obtained under the 0.9 and 1.2 kPa VPD treatments. Growth in the 1.4 and 1.7 kPa VPD environments was 68 and 75%, respectively, of the average growth in the two lower VPD treatments. Transpiration rates were similar across treatments (Fig. 1d); thus, water movement through the plants did not increase in response to increasing VPD.

The lack of a transpiration response to increasing VPD first confirms that soil evaporation was a very small component of the water loss since it would be expected that evaporation would increase with VPD. Instead, the existence of a maximal water loss rate indicates that transpiration rate was under the control of the plants and that the maximum rate allowed by these tall fescue was expressed under all VPD treatments. Such a limitation is likely a result of stomatal closure in response to elevated VPD (Bunce 2006), due to the fact that water transport in the plant could not meet transpirational demand. Stomatal closure, the accompanying restriction of the CO_2 diffusion pathway, and the resulting decrease in photosynthesis likely were responsible for the decreased growth at increased VPD. These results indicate that the maximum water loss in tall fescue is expressed at a VPD $\leq$ 0.9 kPa, a value similar to that observed in experiments with *A. unedo* (Turner et al. 1984).

Results of these experiments have major implications in predicting plant response to climate change. These results show that the common label of tall fescue as a cool season species probably reflects sensitivity to elevated VPD during the warm seasons rather than direct sensitivity to temperature. A full understanding of the growth of this species cannot be gained by solely considering temperature, but VPD must be accounted for due to its critical limitation on growth.

These results have important implications in attempts to predict plant response to climate change. Tall fescue, and perhaps other cool season species, could experience a substantial benefit with temperature increases expected in temperate zones if VPD were to remain unchanged. During the past 50 years, VPD has remained virtually constant (Szilagyi et al. 2001) due to an increase in atmospheric dew point temperature (Gaffen and Ross, 1999; Robinson 2000). This study, therefore, identifies two key questions in assessing the effects of global climate change on plant growth: (1) what is the VPD sensitivity of the specific species being evaluated, and (2) will there be continued stability in VPD

Fig. 1 Weekly growth (**a, b**) and transpiration rates (**c, d**) for well-watered tall fescue plants in two experiments. Panels **a** and **c** are results from various temperature treatments while VPD was held constant at 1.2 kPa. Panels **b** and **d** are results from various VPD treatments while temperature was held constant at 22°C. Standard error of the mean is denoted by bars on each column. Significant differences in growth rate among treatments within each experiment are noted with differing letters ($P < 0.05$). There were no significant differences in transpiration rate among treatments within either of the two experiments



resulting from greater increases in atmospheric dew point temperatures relative to increases in daily maximum temperatures?

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