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The response of mesophyll conductance to nitrogen and water availability differs between wheat genotypes

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ABSTRACT

Increased mesophyll conductance (g_m) has been suggested as a target for selection for high productivity and high water-use efficiency in crop plants, and genotypic variability in g_m has been reported in several important crop species. However, effective selection requires an understanding of how g_m varies with growth conditions, to ensure that the ranking of genotypes is consistent across environments. We assessed the genotypic variability in g_m and other leaf gas exchange traits, as well as growth and biomass allocation for six wheat genotypes under different water and nitrogen availabilities. The wheat genotypes differed in their response of g_m to growth conditions, resulting in genotypic differences in the mesophyll limitation to photosynthesis and a significant increase in the mesophyll limitation to photosynthesis under drought. In this experiment, leaf intrinsic water-use efficiency was more closely related to stomatal conductance than to mesophyll conductance, and stomatal limitation to photosynthesis increased more in some genotypes than in others in response to drought. Screening for g_m should be carried out under a range of growth conditions.

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1. Introduction

Increasing mesophyll conductance (g_m) has been suggested to provide an opportunity to improve water-use efficiency of crops, because a higher g_m will result in higher chloroplastic CO_2 partial pressures, C_c [1,2]. The increase in C_c will allow higher photosynthetic rates, all else being equal, without an increase in transpiration rate, resulting in an increase in leaf intrinsic water-use efficiency (the ratio of photosynthetic rate to stomatal conductance A/g_s). There is growing evidence of genotypic variation in g_m among our important crop species [1,3,4]. The first hints of genetic control of g_m were recently presented for

common wheat, with a region of genetic control of g_m on chromosome 2A [5], raising the possibility of selecting for high g_m to increase A/g_s .

Mesophyll conductance has been shown to respond to environmental conditions, both in terms of long-term, growth conditions, and more recently in response to dynamic changes in environment. Long-term exposure to low light resulted in decreased g_m in walnut [6], maple [7], birch, linden, and the perennial herb goldenrod [8] and in beech [9]. The short-term response of g_m to light is not as clear, with a positive relationship between the two in some species and experiments [10,11] but not others [12]. Similarly, the short-term response of g_m to temperature is variable, with some species showing limited response, and others showing a strong sensitivity of g_m to temperature [13,14].

Both water and nitrogen availability strongly limit photosynthetic rate, the first through reductions in stomatal conductance and the second through lowered photosynthetic capacity. Reduced nitrogen availability has been shown to lower g_m in spinach [15], *Pinus radiata* [16], and rice [17,18]. Moreover, positive correlations were found between leaf N content and g_m in rice [19,20], a range of wheat cultivars [21], and four crop species (rice, wheat, spinach and tobacco) grown under differing N availabilities [22]. In contrast, the response of g_m to limited N availability was small in *Eucalyptus globulus* [23]. In a review of published experiments, Flexas et al. [24] found that water stress often reduced g_m (18 out of 20

Abbreviations: A , photosynthetic rate; A/g_s , leaf intrinsic water-use efficiency; CA , carbonic anhydrase; C_c , chloroplastic CO_2 partial pressure; C_c/C_a , the ratio of chloroplastic to ambient CO_2 partial pressure; C_i/C_a , the ratio of intercellular to ambient CO_2 partial pressure; g_m , mesophyll conductance; g_s , stomatal conductance to water vapour; J_{max} , electron transport rate; S_c , surface area of chloroplasts exposed to the intercellular air space per unit leaf surface area; V_{cmax} , maximum carboxylation rate; VPd , leaf-to-air vapour pressure difference; Δ_i , predicted photosynthetic carbon isotope discrimination assuming infinite mesophyll conductance; Δ_{obs} , measured photosynthetic carbon isotope discrimination; Ψ_L , leaf water potential.

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studies), but more recent work has suggested that reduction in g_m under drought may be transient [25,26]. Decreased g_m in response to reduced water and nitrogen availability may relate to changes in leaf anatomy [20], changes in membrane permeability due to aquaporin expression or activity [25], or differences in chloroplast size or location [17].

Given the observed changes in g_m in response to growth conditions, any breeding program aiming to increase water-use efficiency through g_m must ensure a full understanding of the ranking of genotypes for g_m and A/g_s under a wide range of growth conditions. Here we quantify variation in g_m between wheat genotypes grown under conditions of varying nitrogen and water. We also investigate the stomatal and mesophyll limitations to photosynthesis under the differing growth environments, and assess the relative importance of stomatal and mesophyll conductance on leaf intrinsic water-use efficiency.

2. Materials and methods

2.1. Plant material and growth conditions

Wheat (*Triticum aestivum* L.) plants of the cultivars 'Dart', Gregory', 'Livingston', Spitfire', 'Sunguard' and the pre-release line LPB10-0018 from LongReach Breeding Company were germinated in 6L pots filled with washed river sand, 3 plants per pot. Plants were grown in a controlled environment room at 25 °C and 75% relative humidity during the 14-day light period (photosynthetically active radiation at the upper leaf surface was 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$), and 17 °C and 75% humidity during the 10-h dark period. The CO_2 concentration was controlled at 400 ppm, but frequently increased to 600 ppm during the dark period due to respiration. However, the CO_2 concentration and $\delta^{13}\text{C}$ in the dark have little influence on photosynthetic assimilation. The $\delta^{13}\text{C}$ of CO_2 inside the room during the light period was measured using a stable isotope cavity ring down laser (G11101-i, Picarro CA, USA) and found to be -10.0‰ on average during the week prior to measurements and during the week that measurements were made. This value was used in the calculation of g_m . All pots were supplied with 5 ml of either full nutrient solution (including 10 mM NH_4NO_3 ; high N) or nutrient solution with adequate N but full supply of all other macro- and micro-nutrients (including 4.5 mM NH_4NO_3 ; adequate N) three days a week, and well watered four days a week for four weeks. At this point, limited water availability was applied to half the pots by withholding water on the days that nutrient solution was not applied until 50% of plants had reached temporary wilting point, assessed visually. This occurred after 8 days for high N pots and after 10 days for adequate N plants. The weight of each pot was recorded at this point and designated as the target weight for the pot. Thereafter, the water content of droughted pots was maintained gravimetrically by adding nutrient solution (three days a week) and/or water (every day) to bring the pot to the target weight. This created four growth conditions, namely high N and well-watered, high N and droughted, adequate N and well-watered and adequate N and droughted. Five replicate plants were grown for each genotype in each of the four growth conditions.

Prior to the start of the water availability treatment, plants were thinned to one per pot. One of extra plants was separated into the first leaf (leaf one), the fourth leaf (leaf 4) of the main tiller and the rest of the plant. Leaf gas exchange and water potential measurements occurred on the sixth and seventh weeks, and all plants were destructively sampled at the end of the measurements (eight weeks after planting seeds). At the time of harvest, all plants were pre-anthesis but all had at least some emerged heads. Plants were separated into emerging heads, leaves, stems and roots. Leaves 1 and 4 from the main tiller, plus the youngest fully expanded leaf

were sampled separately. All samples from both harvests were dried at 65 °C for a minimum of 48 h before weighing for biomass. The individual leaves sampled prior to the water treatment and at the final harvest were ground to a fine powder and analysed for total N content (%N) and carbon isotope composition on a stable isotope ratio mass spectrometer (Delta V, Thermo Finnigan).

2.2. Leaf gas exchange and water potential measurements

Photosynthetic CO_2 response curves were measured using a portable gas exchange system (LI-6400xt, LiCor, Lincoln, NE, USA) for three of the six genotypes for all four growth conditions; Gregory, Livingston and Spitfire. The Li6400 was fitted with the standard 2 by 3 cm and red-blue light source. The light source was set to provide 1250 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, leaf temperature was controlled at 25 °C and the leaf-to-air vapour pressure difference (VPd) between 0.75 and 1.0 kPa. The youngest fully expanded leaves from each plant was used for measurements. Maximum carboxylation rate (V_{cmax}) and electron transport rate (J_{max}) were fitted using the spreadsheet from Sharkey et al. [27] but using estimated g_m for each individual leaf. We also used the Sharkey et al. [27] spreadsheet in its original form to fit all parameters, including g_m , for comparison with the fitted parameters using known g_m . CO_2 response curves and estimated g_m values were used to calculate stomatal (L_s) and mesophyll (L_m) limitations to photosynthesis at an ambient CO_2 concentration of 400 ppm using the method described by Warren et al. [28].

A Scholander-style pressure chamber (115, Soil Moisture Equipment, Santa Barbara, CA, USA) was used to measure the water potential (Ψ_L) at midday for all leaves immediately after gas exchange measurements. Leaves were wrapped in plastic film and cut just above the ligule with a razor blade prior to sealing in the pressure chamber for measurement.

2.3. Mesophyll conductance measurements

Mesophyll conductance was estimated using a coupled leaf photosynthesis system (LI-6400xt, as above) and stable carbon isotope tunable diode laser (TGA100A, Campbell Scientific, Logan UT, USA) as described by Barbour et al. [1]. The Li-6400 was fitted with a 2 by 6 cm narrow leaf chamber (Li6400-11) and irradiance provided by a red-green-blue light source (Li6400-18) set to mimic the red-blue light source at an irradiance of 1250 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR. Leaf temperature was controlled at 25 °C and VPd between 0.8 and 1.6 kPa. Two or three of the youngest fully expanded leaves were placed side by side in the leaf chamber.

g_m was calculated from the difference between predicted discrimination assuming infinite mesophyll conductance (Δ_i) and measured discrimination (Δ_{obs}), using equations developed by Evans et al. [29] and Barbour et al. [1], and including a ternary effect as described by Farquhar and Cernusak [30]. We assume values of fractionation factors; carboxylation fractionation was assumed to be 29‰, fractionation during dissolution and diffusion through water was assumed to be 1.8‰, the fractionation associated with photorespiration was assumed to be 16.2‰, the fractionation occurring during diffusion through the leaf boundary layer was assumed to be 2.9‰ and the rate of day respiration was taken to be 1.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (from Jahan et al. [4]).

2.4. Statistical analysis

Differences between the various physiological measures were assessed using general analysis of variance, as implemented by GenStat 14th edition, and means were compared using Bonferroni significant difference test. Differences were considered statistically

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