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Does higher yield potential improve barley performance in Mediterranean conditions? A case study

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Abstract

Barley is one of the most widely cultivated crops in rainfed areas of the Mediterranean, where drought is the main factor that limits yield. Knowledge of the physiological traits responsible for adaptation of barley cultivars to Mediterranean environments may be relevant for future breeding strategies. Yield potential versus drought tolerance is an open debate. Here, we studied two barley cultivars (Graphic and Kym), of similar time to anthesis and crop duration, that are widely cultivated in the western Mediterranean. Grain yield was evaluated in 41 field trials and ranged (averaged for the 16–32 cultivars assayed in each trial) from 0.7 to 9.1 Mg ha^{-1}. Yield components and carbon isotope discrimination ($\Delta^{13}C$) of grains was analysed in another two trials. Graphic production was greater than Kym in all conditions. This greater yield was sustained mainly by more ears per unit ground area, which may be attributable to higher growth potential during tillering. Moreover, Graphic showed greater $\Delta^{13}C$ of kernels, indicating improved water status even at the end of the crop cycle. To examine differences in early growth, these cultivars were grown in optimal conditions and then photosynthetic activity and biomass analysed at the end of tillering. Graphic showed greater above-ground and root biomass as well as total leaf area per plant and per tiller than Kym, and also tended to have more tillers per plant, but its shoot-to-root biomass ratio was lower. Nitrogen content per unit leaf area was correlated negatively with plant and with tiller leaf area and positively with the shoot-to-root biomass ratio. Photosynthetic rate per unit leaf area was lower in Graphic and positively related to a lower nitrogen content, whereas stomatal limitation of photosynthesis and water use

Abbreviations: A, net CO_2 assimilation rate; A_{max}, CO_2-saturated net CO_2 assimilation rate; A_{sat}, light-saturated net CO_2 assimilation rate; c_a, c_i, ambient and intercellular CO_2 concentration, respectively; DW, dry weight; $\Delta^{13}C$, carbon isotope discrimination; F_m and F'_m, maximum fluorescence in dark-adapted and light-adapted leaves, respectively; F_v/F_m, maximum efficiency of PSII photochemistry after dark-adaptation; F'_v/F'_m, efficiency of energy capture by open PSII centers; F'_o, minimum fluorescence yield in light-adapted state; ϕ_{PSII}, quantum yield of PSII electron transport; g_s, stomatal conductance; $J_{max,RuBP}$, maximum potential rate of electron transport contributing to ribulose 1,5-biphosphate regeneration; $J_{max,PSII}$, the rate of PSII electron transport in saturating light and CO_2; l, stomatal limitation to A_{sat}; PPFD, photosynthetic active photon flux density; PSII, photosystem II; q_P, photochemical quenching of chlorophyll fluorescence; R_d, dark respiration; RuBP, ribulose 1,5-bisphosphate; RWC, relative leaf water content; TR, transpiration rate; $V_{c,max}$, maximum carboxylation velocity of Rubisco; WUE, water use efficiency; ψ_w, leaf water potential.

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efficiency was similar in the two cultivars. Ribulose 1,5-biphosphate regeneration capacity contributed to the lower photosynthetic rate of Graphic. Moreover, quantum yield of photosystem II (PSII) electron transport was also lower in Graphic than Kym, which suggests that mechanisms other than leaf structure also contributed to the higher photosynthetic capacity of the former. Nevertheless, as result of differences in leaf area, total plant photosynthesis was greater in Graphic.

The results indicate that the higher yield of Graphic under a wide range of Mediterranean conditions may be sustained by increased plant growth and total photosynthesis during tillering, although the photosynthetic capacity per unit leaf area is lower than that of Kym. Graphic has a more extensive root system than Kym, subsequently improving its water status in later stages of the crop cycle. Nitrogen content per unit leaf area is a good indicator of the growth and photosynthetic activity of barley plants in the early stages of the crop cycle.

Keywords: Barley; Chlorophyll fluorescence; Drought; Net CO_2 assimilation; Grain yield; *Hordeum vulgare*; $\Delta^{13}C$; Carbon isotope discrimination; Water use efficiency

1. Introduction

Plant growth and yield are severely reduced by water deficit, drought being the main abiotic stress factor that limits the production of cereals and other major crops in Mediterranean conditions (Acevedo et al., 1999; Araus, 2002). Barley is one of the most widely cultivated cereals in the Mediterranean region, where it is grown even in the driest areas.

Knowledge of the traits responsible for adaptation of barley to Mediterranean environments may be relevant for future breeding strategies. In Mediterranean rainfed conditions, genetic improvement through breeding is frequently hindered by a large interaction between genotype and environment (either season or location), which mainly arise from unpredictable rainfall (Richards et al., 2002). Thus, when grown under harsh environments, the genotypes selected for poor environmental conditions probably perform better than those released for high-yielding environments and vice versa. From an ecophysiological perspective, drought responses may be initially divided into two categories: those that confer tolerance to extreme stress, and those that maximize productivity under less extreme conditions. Drought tolerance may incur penalties in yield under less extreme conditions, while traits maximising productivity are fully expressed in the absence of stress (i.e. constitutive traits) although they still sustain yields under mild to moderate drought (Blum, 1996; Araus et al., 2002a). Thus, for growing areas other than the very drought-prone environments proposed barley ‘‘ideotypes’’ should have minimal genotype by environment interaction, showing both high yield potential and yield stability. Hence, selection for greater yield potential has frequently resulted in higher production in a wide range of environments (Slafer et al., 1999; Richards, 2000; Richards et al., 2002; Araus et al., 2002a). However, for drought-prone environments with barley yields often below 1.0 Mg ha^{-1}, breeding efforts to improve survival (i.e. tolerance to severe stress) and thus yield stability have been successful (Ceccarelli and Grando, 1996). In these conditions, locally adapted germplasm has been used (Ceccarelli et al., 1998). Therefore, there is a general agreement that for barley a high yield potential is advantageous under moderate stress conditions, whereas advantages from drought tolerance of a cultivar with low yield potential may be expressed only when stress is severe (Voltas et al., 1999).

Fast growth before anthesis is important in a Mediterranean climate, where terminal drought during the spring is probable (López-Castañeda et al., 1995). This trait may explain the relative success of barley in these environments. The advantage of early-growth stems from higher water use efficiency because growth take place when it is cool (winter) and less water is lost from the soil surface (e.g. Blum, 1996). Although high yield potential and drought tolerance have been considered mutually exclusive (e.g. Blum, 1996), greater biomass accumulation before anthesis could be compatible with both traits (López-Castañeda et al., 1995).

Plant growth is affected by the amount of photosynthetically active radiation intercepted (which depends on leaf area) and the efficiency with which radiation (RUE, i.e. photosynthetic rate/PPFD) is converted (Smith et al., 1999). Although the contribution of photosynthetic rate to final grain yield is