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The contribution of ear photosynthesis to grain filling in bread wheat (*Triticum aestivum* L.)

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A B S T R A C T

The contribution of ear photosynthesis to grain filling in wheat (*Triticum aestivum* L.) is not well known. The main objective of this work was to evaluate this contribution through three different experimental approaches: (1) ear photosynthesis was reduced by removing awns or shading the ears (in combination with a defoliation treatment), (2) grain weight per ear was compared in an ‘all shaded’ crop *versus* plants where only the vegetative parts were shaded (‘ear emerging’), and (3) ear photosynthesis was reduced with DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea), a specific inhibitor of photosystem II.

In field experiments in La Plata (Argentina), cultivars Klein Escudo and BioINTA 3000 were subjected to awn removal and ear shading treatments, with or without severe defoliation, and to ‘all canopy shaded’ *versus* ‘ear emerging’ treatments. Although the estimated contribution of ear photosynthesis to grain yield differed depending on the experimental approach used (from about 12–42%), in general cv. Klein Escudo (with the largest awns) showed a greater contribution of ear photosynthesis. In both cultivars, the percentage contribution of ear photosynthesis was larger for defoliated plants. The magnitude of this contribution was positively associated with the length of awns of each cultivar. Awn removal had a non-significant ($p \leq 0.05$) effect on grain weight per ear (GW_{ear}) in the short-awned cv. BioINTA 3000. In cv. Klein Escudo, the effects of de-awning were larger, reaching values of *ca.* 15 and 19% decrease of GW_{ear} in non-defoliated and defoliated plants respectively. In both cultivars, grains in a distal position within the spikelet (G3) were most affected by the decrease of the photosynthetic source. The photosynthetic rate of the ear was higher in cv. Klein Escudo than in cv. BioINTA 3000.

We analyzed the contribution of remobilization of pre anthesis assimilates (stem *plus* sheaths). Comparing both cultivars, dry matter translocation from the stem showed the opposite pattern to the contribution of ear photosynthesis, i.e. it was higher in cv. BioINTA 3000 than in Klein Escudo.

In Bordenave, Argentina, ear shading treatments revealed an important contribution of ear photosynthesis to grain yield in cv. Huenpan (a long awned, water-deficit tolerant genotype), either under water deficit or irrigation, whereas in cv. Baguette Premium 11 (short awns) there was apparently no effect of ear photosynthesis on yield.

Finally, inhibition of ear photosynthesis with DCMU reduced grain weight per ear to a similar extent as ear shading.

Ear photosynthesis might represent a “buffer” to maintain grain yield under source limitations (e.g. defoliation, water stress conditions), and could have an important role even without stress, because an incipient ‘source’ limitation might be emerging in modern cultivars of bread wheat.

1. Introduction

In C_3 cereals, such as wheat and barley, grain filling is sustained by current photosynthesis of the upper parts of the plant, i.e. the flag and penultimate leaves *plus* the ear (see Tambussi et al., 2007 and references cited therein) and by redistribution of assimilates stored in the stem (Blum, 1998; Foulkes et al., 2007; Ehdaie et al., 2008; Álvaro et al., 2008a). Although several studies analyzed ear photosynthesis from a physiological viewpoint (see references in Tambussi et al., 2007), its contribution to grain filling is not clear. In fact, compared with other sources of assimilates, the photosynthetic contribution of green parts of the ear (glumes, lemmas, awns and pericarp) has been less studied.

Grain yield of wheat is often limited by the strength of the sink rather by the availability of assimilates (i.e. the ‘source’, Slafer and Savin, 1994). Although this limitation due to sink capacity depends

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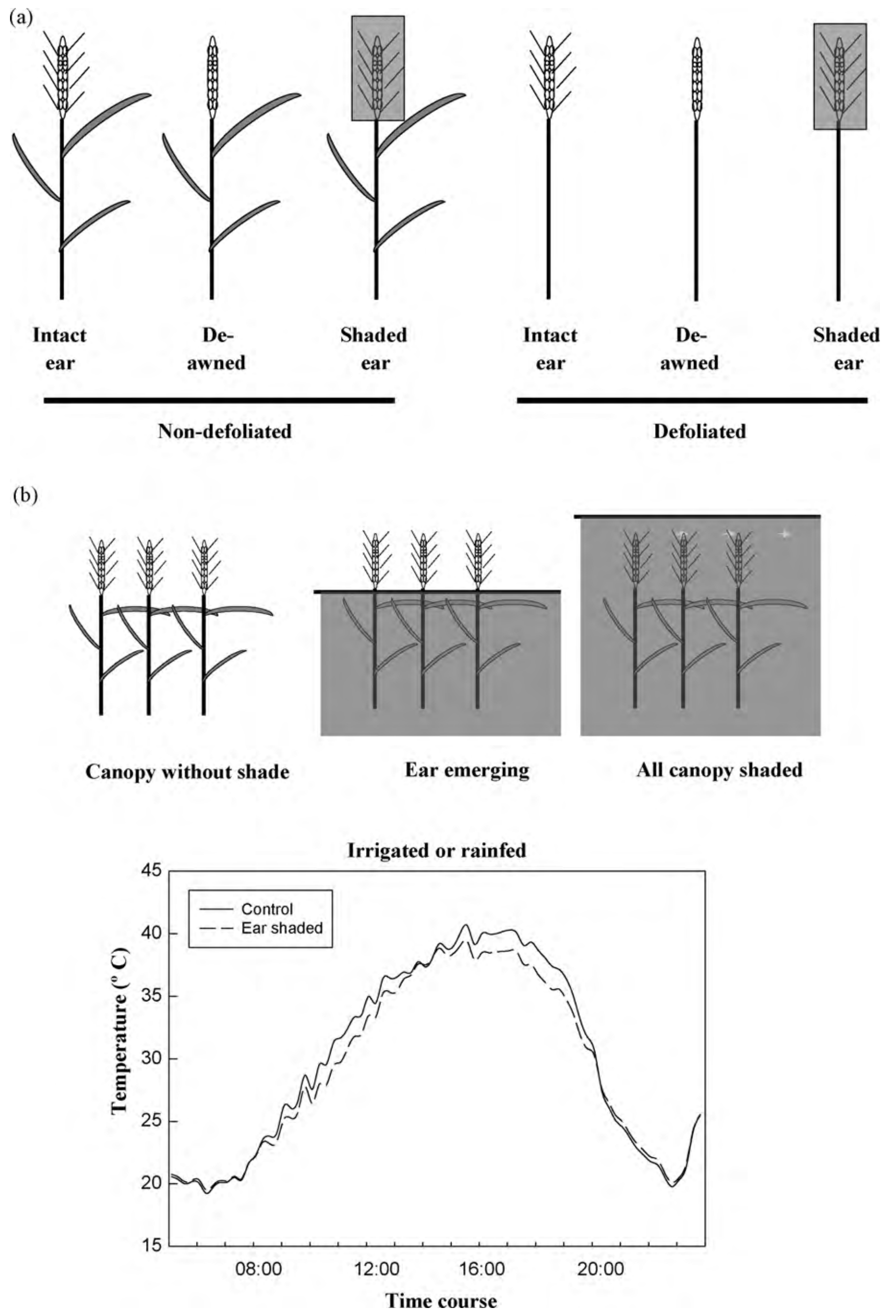

Fig. 1. Diagrams showing the experimental set-up for the awn removal, ear shading, defoliation (*panel a*) and the crop shading (*panel b*) experiments. All the treatments in both experiments were imposed five-seven days after anthesis. Shading of the ear (upper diagram) was made with a perforated aluminum foil. The shade in the second experiment had a transmittance *ca.* 10%. *Panel c.* Diurnal course of temperature of control (i.e. non-shaded) ears, and ears shaded with aluminum foil. Temperature was measured every fifteen minutes with thermocouple sensors placed beneath the glumes. Each line is the mean of eight ears per treatment.

on the environment (Blade and Baker, 1991), if there is an excess of assimilates during grain filling (Borrás et al., 2004), the photosynthesis of ear parts could be of minor importance. However, recent evidences indicate that some limitation by source could be emerging in modern cultivars of wheat (e.g. Álvaro et al., 2008a).

In winter cereals, e.g. wheat, water deficit is a common abiotic stress that reduces grain yield (Araus et al., 2002). Water stress decreases photosynthetic rate (e.g. Lawlor, 2002) and accelerates leaf senescence (Martinez et al., 2003). Compared with the flag leaf, the photosynthetic rate of the ear parts is reduced to a lesser extent under water stress in durum (Tambussi et al., 2005) and bread wheat (Martinez et al., 2003). Although the apparent drought 'tolerance' of ear photosynthesis is not completely understood, it seems to be associated with the ability to maintain a higher relative water content in glumes, lemmas and awns (Tambussi et al., 2005). Moreover, ear bracts and the kernel pericarp can refix the CO_2 emitted by growing grains (Bort et al., 1994; Gebbing and Schnyder, 2001). Under drought conditions, the ear may become the main source of photosynthates for grain filling in barley (Bort et al., 1994; Sánchez-Díaz et al., 2002) and durum wheat (Araus et al., 1993; see also references in Tambussi et al., 2007).

In bread wheat the contribution of ear photosynthesis to grain yield is poorly understood. One reason for this is that the photosynthetic contribution of the ear is not easy to measure, in particular in field trials. The main objective of this work was to assess the contribution of ear photosynthesis to grain yield of bread wheat (using