



Below- and above-ground growth and biomass allocation in maize and *Sorghum halepense* in response to soil water competition

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Summary

The aim of this study was to establish the morphological or physiological nature of the changes in growth parameters of maize and *Sorghum halepense* plants growing under competition for water. Plant growth analysis studies in semi-controlled conditions in plastic containers were conducted in two consecutive years. The competition treatments were established 4 weeks after emergence of both species and lasted for 4 weeks. Treatments of low (75% of field capacity) and very low water availability (irrigation withheld) were established. The variables obtained were: relative growth rate (RGR), leaf area ratio (LAR), net assimilation rate (NAR), specific leaf area (SLA), leaf mass fraction (LMF), rhizome mass fraction (rizMF), root length ratio (RLR), root mass fraction (RMF), specific root length (SRL) and length of fine roots (VfRL). The RGR of

S. halepense was less affected by the two levels of competition than that of either of two maize hybrids. The weed was able to maintain its ability to grow, due to the maintenance of NAR during competition. A similar contribution of biomass from leaves and rhizomes to roots was observed in *S. halepense*, favouring the formation of very fine roots. In contrast, in maize, the decrease in RGR was due to a decline in NAR and there was no formation of fine roots to maintain water absorption during competition. The greater increase both in biomass partitioned to roots and root length by *S. halepense*, might negatively impact maize ability to compete for water during the critical competition period.

Keywords: *Zea mays*, Johnson-grass, plant growth analysis, aerial and root growth, mechanism of competition, competitive ability, RGR.

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Introduction

Maize (*Zea mays* L.) production is an important component of Argentinian agriculture, with annual exports of US\$ 2100 million (Senasa, 2007). This production is obtained mostly under dryland farming, where the alternation of humid and dry soil periods is frequent. Weed competition is one of the major constraints to Argentinian maize production (Ghersa,

2000). Under these farming conditions, water is usually a limiting resource for crop and weed growth (De Abelleira *et al.*, 2008).

Sorghum halepense (L.) Pers. (Johnson-grass) is one of the world's worst weeds (Holm, 1977) and has proved hard to control in the extensive cropping systems of Argentina (Leguizamón, 1999), despite the use of glyphosate-resistant soyabean cultivars. Satorre *et al.* (1985) have shown that maize yield losses varied

between 12 and 95% due to weed competition. The competitive ability of *S. halepense* in agricultural systems of the Argentine Rolling Pampas, as well as several ecophysiological and demographical features of this species, have been evaluated in different studies (Vila-Aiub *et al.*, 2007). In recent years, populations of *S. halepense* have been confirmed as glyphosate resistant in Argentina (Vila-Aiub *et al.*, 2007). The risk of resistance to glyphosate, and other factors such as heightened environmental awareness, have drawn attention to the design of ecologically based weed management programmes that focus on how factors, such as resource availability, climate and edaphic properties, will affect the competitiveness of maize and *S. halepense*.

Competition for water is one of the most important processes that cause water stress, resulting in reductions in both weed growth and crop yield. Although many studies document the impact of water availability on the outcome of maize-weed competition (Tollenaar *et al.*, 1997), the mechanisms by which water availability mediates competitive relationships are only partially understood.

Changes in morphological and physiological traits of maize under competition with weeds for light and nutrients have been documented (Mohammadi, 2007), but the actual mechanism of water competition between maize and *S. halepense* has received no attention.

The techniques of plant growth analysis provide a useful tool to determine the competitive mechanism between weeds and crops, when grown in mixtures (Mohammadi, 2007). Relative growth rate (RGR) can be split into two components, the net assimilation rate (NAR) and the leaf area ratio (LAR) (Poorter, 1989). LAR can be further decomposed into specific leaf area (SLA, a measure of leaf thickness) and leaf mass fraction (LMF, leaf mass as a fraction of shoot mass). Evaluation of below-ground characteristics is problematic, because of the complexities of soil-plant interactions and the difficulty of defining root structural features *in situ*. Root acquisition of water and nutrients depends more on root length or root surface area, than on root mass (Eissenstat, 1997) and is closely related to the soil volume that plants explore and the thoroughness of exploitation (Ryser, 1998). Both these aspects can be maximised with a long root system, which can be achieved by a high root length per total plant dry mass (root length ratio, RLR) (Ryser & Eek, 2000). The RLR is determined by the relative allocation of biomass to the roots (root mass fraction, RMF) and by the root length per unit root dry mass (specific root length, SRL) (Ryser, 1998).

In short-term competition experiments (no more than one growing season) carried out with a limiting supply of soil resources, species with a high RGR have shown a greater competitive ability associated with a higher SRL.

Moreover, a highly positive correlation between RMF and NAR was reported (Konings *et al.*, 1989; Shipley & Meziane, 2002). Thus, given the large effects of water deficit on LAR (Lambers *et al.*, 1998) and the tendency to distribute photoassimilates preferably towards the roots (higher RMF), species with this growth strategy might develop a higher water absorption capacity (relative to their transpiration needs) under conditions of low water availability. The plasticity in SRL was related to the capacity for absorption of soil resources, which is related to the plant's competitive ability for soil resources (Eissenstat *et al.*, 2000). Thus, under below-ground competition, a greater competitive ability might be expected for those species characterised by a high RMF and/or a high SRL. This may lead to a larger RLR and, consequently, this should contribute to the maintenance of NAR (Derner & Briske, 1999).

Despite the importance of competition for water in maize and *S. halepense* (Stuart *et al.*, 1985; Mohammadi, 2007), no studies have addressed below- and above-ground growth analysis and biomass allocation in these species when grown in mixture under a soil water competition regime. Understanding how soil water competition affects maize and *S. halepense* below- and above-ground growth responses is necessary, in order to design maize management strategies to reduce the negative effects of the weed.

The objectives of this study were to determine the relationship of both growth parameters, NAR and LAR with the relative growth rate, and of RMF and SRL with the root length ratio of two simple hybrids of maize and *S. halepense*, during the vegetative growing cycle under soil water competition. The broader objective was to gain a more complete understanding of growth strategies of maize and *S. halepense*, to facilitate management of crops growing under soil water competition.

Materials and methods

This study was carried out in the Agrarian and Forest Sciences Faculty (La Plata National University), La Plata (34°S, 58°W, Argentina), during the growing period October–February of 2003–2004 and 2004–2005.

Plants were grown in pots (84 L: 60 cm long × 40 cm wide × 35 cm deep) placed under a rain shelter (a roof of transparent polyethylene, 200 µm thick, placed 3 m above the plants) to avoid rainfall. Pots were filled with a sand, soil and peat moss mixture (35:25:40 *V/V* respectively). The texture of this mix allowed the separation of the roots of both species. Each pot was fertilised with 230 mg of N applied as urea and 285.2 mg of P₂O₅ applied as calcium triple superphosphate at planting. The final composition of the substrate was 3.05% of organic matter, 2.15% of organic carbon,

0.24% of total nitrogen, 32.5 mg kg⁻¹ of nitrate, 13.8 mg kg⁻¹ of available phosphorus (Bray Kurtz II) and a pH of 6.2. The water retention values of the substrate were: 0.45 cm³ cm⁻³ of water at a soil water potential of 0.001 MPa, 0.25 cm³ cm⁻³ at 0.02 MPa and 20 cm³ cm⁻³ at 0.2 MPa.

Plant material and growth conditions

Rhizomes of *S. halepense* were originally collected in March 2003 as vegetative propagules from agricultural fields in the vicinity of La Plata. Following completion of experiments each autumn, newly produced propagules were planted in 50 L pots and maintained outdoors. These rhizomes grew vigorously and produced a large supply of new propagules that were used for experiments the following spring. The rhizomes were trimmed to pieces with two nodes, weighing from 5 to 8 g. All propagules were washed free of soil and then soaked in a solution of 0.30 g L⁻¹ benomyl (methyl 1-[butylcarbamoyl]-2-benzimidazolecarbamate) (Iperlate WP; Ipsesa) for 10 min to reduce decay. Rhizomes were then layered in moist vermiculite and held in a growth chamber at 28°C (Horowitz, 1972). Four sprouted buds per pot were planted simultaneously with maize hybrids on 5 October 2003 and 8 October 2004.

Two maize hybrids (Ax888 and Ax840) of intermediate cycle with 1572 and 1535 growing day degrees (d°C; 8°C base temperature) to physiological maturity (R₆, Ritchie & Hanway, 1982) were used. Ax888 is characterised by a plant height of about 2.00 m and is adapted to high availability of soil resources. Ax840 is a shorter (plant height of about 1.70 m) hybrid and is adapted to soil limited conditions. Eight seeds, pre-germinated in Petri dishes, were sown in each pot and thinned to four plants per pot at V₂ (second leaf completely expanded). Pots were watered every day (soil water potential = -0.03 MPa) up to 21 days after emergence (DAE), when treatments of low (L, 75% of field capacity, approximately -0.04 MPa) and very low water availability (VL, irrigation withheld) were established. The experiment lasted 24 days (up to 45 DAE), which corresponded with the maize critical period of weed competition (V₄-V₇) (4-7-leaf expanded period). The soil surface in the very low water availability treatment pots was covered with polystyrene beads to minimise soil evaporation. Control pots were watered daily in order to maintain the soil water content near to -0.03 MPa (field capacity), determined by means of a water potential probe (Thermolink soil multimeter; Decagon Devices, Pullman, USA). The treatments were: genotypes (maize hybrids and *S. halepense*) and water availability (control, low and very low water availability). A 1:1 additive design arranged in a randomised

complete block design was used, i.e. the density (four plants per pot) of each species in mixture is the same as that in the monoculture. Three replicates per treatment (with one pot as an experimental unit) were employed.

Measurements and variables

Seven measurements were carried out every 4 days, in order to estimate RGR for the competition period. Above-ground plant parts were harvested, separated into leaves (leaf blades), stems, rhizomes (*S. halepense*), and inflorescences (after the fourth measurement) and dried at 48°C (constant weight) for dry matter determination (g plant⁻¹). A modification of the methods employed by Siddique *et al.* (1990) and Novoplansky and Goldberg (2001) was applied for root sampling. After cutting off above-ground plant parts, the pot soil block was first completely immersed in a sodium hexametaphosphate (Calgon, Fisher) (5% wt/V) solution for 48 h. The root systems of both species were gently separated; not more than 5-6% of total root weight remained unidentified in each pot. Each sample was placed in a plastic bag and frozen until analysis. Samples were defrosted and soil was removed using a root washer unit, based on a hydropneumatic elutriation system (Delta T Devices, Cambridge, UK). To collect the roots, 2 mm and 500, 240 and 100 µm sieves were used to prevent the loss of fine roots. Root length of each sample was determined using the method proposed by Costa *et al.* (2000). For image acquisition, roots were floated in shallow water (2-4 mm) in clear trays (200 by 300 mm) mounted on the scanner bed. Images were captured as 256 levels grayscale with a Hewlett Packard Scan Jet 7400c (Hewlett Packard, Palo Alto, CA, USA). The pixel size was 0.085 mm pixel⁻¹ (300 dpi resolution). Scans were stored as TIFF files. The images were processed with the Delta-T Devices scan software system (Delta-T Devices, Cambridge, UK). Specific root length (SRL) was calculated for the whole root sample, whereas the determination of very fine roots length (VfRL) was obtained on the samples between 100 µm and 240 µm (Pallant *et al.*, 1993). Samples were then dried in an oven at 48°C to constant weight. Both, root length and root dry weight was obtained on a per plant basis (m plant⁻¹; g plant⁻¹).

At each harvest, leaf areas were determined by a LI-COR LI 3100 (Lincoln, NA, USA) leaf area meter. Plant growth analysis was carried out following the procedure of Wickens and Cheeseman (1988) and Poorter (1989). Data of plant biomass and leaf area were used to calculate the RGR (mg g⁻¹ day⁻¹), NAR (mg dm⁻² day⁻¹), LAR (dm² leaf g⁻¹ pl), SLA (dm² leaf g⁻¹ leaf), LMF (g leaf g⁻¹ pl), RLR (m root g⁻¹ pl), SRL (m root g⁻¹ root) and VfRL (m pl⁻¹).

The allocation of biomass to different plant organs was determined as proposed by Poorter and Nagel (2000). According to this, total biomass allocation was divided in four compartments: leaves, stems, rhizome (in the case of *S. halepense*) and roots. Allocation was characterised by fractions expressing the biomass of each organ relative to that of the whole plant: leaf mass fraction (LMF, foliar biomass/total biomass, g leaf g⁻¹ plant), stem mass fraction (SMF, stem biomass/total biomass, g stem g⁻¹ plant), rhizome mass fraction (RhizMF, rhizome biomass/total biomass, g rhizome g⁻¹ plant) and root mass fraction (RMF, root biomass/total biomass, g root g⁻¹ plant). The sum of all fractions adds up to 1. The analysis of LMF, SMF, RhizMF and RMF allocation was performed for the plants grown under competition in the low (L) and very low water availability (VL) treatments, with respect to their controls (absence of competition) according to following the expressions: difference in leaf biomass allocation: (LMF control – LMF L) and (LMF control – LMF VL); difference in stem biomass allocation: (SMF control – SMF L) and (SMF control – SMF VL); difference in root biomass allocation: (RMF control – RMF L) and (RMF control – RMF VL); difference in rhizome biomass allocation (*S. halepense*): (RizMF control – RizMF L) and (RizMF control – RizMF VL). LMF, SMF, RhizMF and RMF allocation were calculated for 25, 28, 32, 37, 41 and 45 DAE.

Resource complementarity

Relative yield total (RYT, De Witt & Van Den Bergh, 1965) was used as a measure of resource complementarity. This index shows the extent to which maize and weeds shared common limiting resources. It is defined as:

$$RYT = (Y_{ij}/Y_{ii}) + (Y_{ji}/Y_{jj}) \quad (1)$$

where Y_{ij} and Y_{ji} are the above-ground biomass per plant of species i (maize) and j (*S. halepense*) when grown in mixture with each other, and Y_{ii} and Y_{jj} are their above-ground biomass when grown in monocultures.

Statistical analysis

Differences between genotypes and water availability were tested by combined analysis of variance of the ln-transformed plant dry weight data (Poorter & Lewis, 1986). A significant interaction between treatments and time indicates a difference in growth parameters through the analysis of the sum of squares of interaction (Poorter & Lewis, 1986). Standard error was used to analyse treatment effects. In this analysis, time was measured as number of days instead of harvests, because time courses did not differ for the two species. Percentages of

fractional biomass allocation were transformed following the expression arcsine of square root of fraction, to improve homogeneity of variance, but data were back-transformed for presentation (Ryser & Eek, 2000). Analyses of variance were also performed on RYT values. Residuals plots indicated that the variance of this variable was normally distributed and homogenous. The statistical package Statgraphics plus 5.1 (StatPoint Technologies Inc., Warrenton, VA, USA) was used to perform analyses.

Results

Treatment by year interactions showed no significant differences ($P = 0.42$), so data across years were combined to show the 2-year averages.

Resource complementarity

For both years, RYT values were not significantly different from 1.0 at each sampling date for both competition treatments (Table 1).

Growth analysis

The two water availability levels reduced RGR, much more in maize than in *S. halepense*. The effect was larger for low water availability level, with the Ax840 showing a higher RGR than the Ax888 hybrid for the study period (Fig. 1B). In *S. halepense*, competition with Ax840 produced the highest decrease of the RGR during the whole competition period (Fig. 1A).

In *S. halepense*, competition with any of both hybrids produced a significant decrease of NAR, compared with the respective monoculture (Fig. 1C). In maize, both competition levels produced a decrease of NAR in both hybrids, although the Ax888 hybrid showed a lower NAR than the Ax840 hybrid throughout the whole competition period (Fig. 1D). In maize, NAR started to decrease after only 4 days (28 DAE) of very low water availability, and it reached very low values after 45 DAE. In contrast, the decline of NAR was gradual, and NAR was maintained at much higher levels under very low water availability in *S. halepense*.

In *S. halepense* the Ax840 hybrid reduced LAR during the whole evaluation period, at both water availability levels. The Ax888 hybrid affected *S. halepense* LAR only in the very low water availability treatment (Fig. 1E). Weed competition affected more intensely the Ax840 hybrid (exponential decrease at the beginning of the competition period). Under very low water availability, there were no differences between the hybrids in LAR decrease (Fig. 1F).

Table 1 Resource complementarity (RYT) in competition [at low (L) and very low (VL) water availability] of *Sorghum halepense* with maize (Sh/Ax840 and Sh/Ax888) at 24, 28, 32, 37, 41 and 45 days after emergence (DAE) in 2003–2004 and 2004–2005.

RYT	2003–2004						2004–2005					
	DAE						DAE					
	24	28	32	37	41	45	24	28	32	37	41	45
Sh/Ax840 (L)	1.08 ± 0.05	1.00 ± 0.04	1.01 ± 0.01	1.04 ± 0.06	1.05 ± 0.06	1.06 ± 0.10	1.02 ± 0.01	1.03 ± 0.01	1.05 ± 0.03	0.99 ± 0.02	1.04 ± 0.02	1.03 ± 0.08
Sh/Ax888 (L)	1.07 ± 0.03	1.05 ± 0.06	1.04 ± 0.05	1.06 ± 0.05	1.06 ± 0.07	1.05 ± 0.09	1.07 ± 0.04	1.04 ± 0.04	1.05 ± 0.02	1.03 ± 0.01	1.03 ± 0.03	1.04 ± 0.06
Sh/Ax840 (VL)	1.07 ± 0.08	0.99 ± 0.07	1.00 ± 0.05	1.01 ± 0.03	1.00 ± 0.04	1.04 ± 0.05	1.07 ± 0.01	1.05 ± 0.03	1.03 ± 0.02	0.99 ± 0.01	1.00 ± 0.03	1.01 ± 0.07
Sh/Ax888 (VL)	1.08 ± 0.04	1.03 ± 0.04	1.02 ± 0.02	1.01 ± 0.02	1.02 ± 0.05	1.00 ± 0.06	1.06 ± 0.05	1.05 ± 0.03	1.02 ± 0.03	1.00 ± 0.02	1.01 ± 0.03	1.00 ± 0.05

Values are mean ± SE (*n* = 3).

Changes in leaf characteristics

The evolution of SLA in *S. halepense* was not affected by the different competition treatments (Fig. 2A). In maize, both weed competition levels reduced SLA in both hybrids early after the onset of water deprivation. Then, SLA values remained constant throughout this period for both levels of water availability (Fig. 2B).

Maize competition affected the LMF in *S. halepense* towards the end of the period of evaluation. When the effect of very low water availability is analysed, there is a trend for a larger decrease in the weed LMF by Ax840 than by Ax888, which is only significant on the 37th DAE (Fig. 2C). In both treatments, the competition exerted by the weed produced a decrease of LMF in Ax840, starting from the first week of evaluation (Fig. 2D).

Adjustment of root morphology

A substantial increase of RLR in *S. halepense* in competition with both hybrids was observed. The RLR increase in the very low water availability treatment was higher than in the low water availability treatment (Fig. 3A). RLR increased only in the maize Ax840 hybrid in the very low water availability treatment, after the 41st DAE (Fig. 3B).

There were differences in the allocation of assimilate to the roots between the control and the water availability treatments in *S. halepense*, although the allocation pattern was not modified by the hybrids with which *S. halepense* was competing (Fig. 3C). While RMF decreased during the period studied in control plants, competition for water delayed this decline (low water availability) or even led to an increase of RMF (very low water availability). Conversely, maize only showed a significant adjustment in the RMF of the Ax840 hybrid for both water availability levels between 32 and 41 DAE (Fig. 3D).

An important variation in the SRL of *S. halepense* was determined during the competition period, with a larger increase for the treatment of very low water availability (Fig. 3E). In maize, a smaller increase in the SRL than that in *S. halepense* was observed. The increase in the SRL was only significant in the Ax840 hybrid (Fig. 3F).

The analysis of the VfRL shows a significant increase in *S. halepense* in the two levels of water availability, starting at 37 DAE, while maize hybrids showed no significant variation of VfRL in competition with *S. halepense* (Fig. 4A and B).

Biomass allocation

From the first week of competition, *S. halepense* allocated more biomass towards the roots when competing

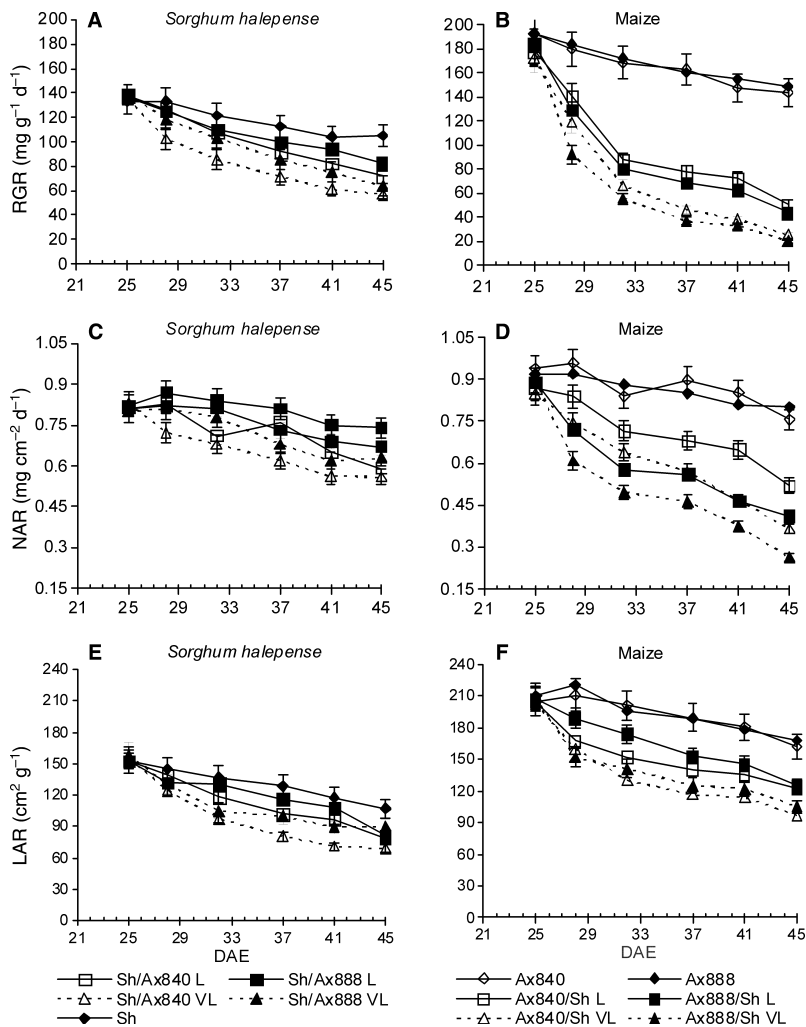


Fig. 1 Time course (days after emergence, DAE) of relative growth rate (A, B: RGR, mg g⁻¹ d⁻¹), net assimilation rate (C, D: NAR, mg plant cm⁻² leaf d⁻¹) and leaf area ratio (E, F: LAR, cm² leaf g⁻¹ plant) of *Sorghum halepense* (Sh) (A, C and E) and two hybrids of maize (Ax840, Ax888) (B, D and F) grown alone or in competition at two levels of water availability (low, L and very low, VL). Values were averaged over two growing seasons. Vertical bars indicate standard error (SE).

with the Ax840 hybrid (Fig. 5A). The increase in biomass allocation to roots after 12 days of very low water availability was highly significant for *S. halepense* growing in mixture with both hybrids of maize (Fig. 5C) and this was maintained during the whole competition period (Fig. 5E and F). Less biomass partitioning towards the rhizome was observed in the very low water availability treatment after 38 DAE (Fig. 5D), while in the low water availability treatment, rhizome biomass allocation was lower up to the third week of the tested period (Fig. 5E and F). Biomass distribution towards the stem was lower in the very low water availability treatment towards the end of the period of evaluation.

With regard to biomass distribution in maize, in the very low water availability treatment, higher biomass allocation towards the roots was observed at the first week of the competition period in the Ax840 hybrid (Fig. 6B, D–F). Ax888 showed a higher biomass allocation towards the roots in both levels of water availability after 43 DAE (Fig. 6E and F). Very low water availability affected biomass distribution towards the stem and reproductive structures (tassel) of maize at

the third and fourth week of established the competition in Ax888 (Fig. 6E) and Ax840 (Fig. 6F) respectively.

Discussion

Resource Complementarity

Maize hybrids and *S. halepense* were fully in competition under the two water levels tested. The RYT values coincide with those found in other soil resource competition studies (Acciaresi *et al.*, 2003), indicating the competition achieved during the vegetative period of both species. It is important to emphasise that in the low water availability treatment, which was maintained at 75% of field capacity, there was a lack of complementarity of resources.

Growth analysis – Relative growth rate

The use of growth analysis to study the competitive association between maize and *S. halepense* allowed the quantification of the change in RGR and also the

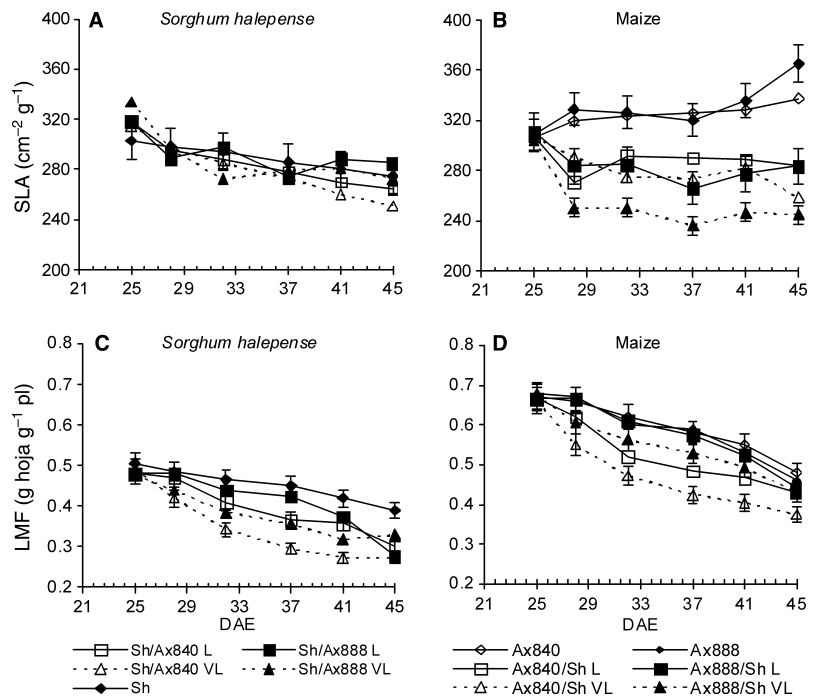


Fig. 2 Time course (days after emergence, DAE) of specific leaf area (A, B: SLA, cm² leaf g⁻¹ leaf) and leaf mass fraction (C, D: LMF, g leaf g⁻¹ plant) of *Sorghum halepense* (Sh) (A and C) and two hybrids of maize (Ax840, Ax888) (B and D) grown alone or in competition at two levels of water availability (low, L and very low, VL). Values were averaged over two growing seasons. Vertical bars indicate standard error (SE).

changes in the components that comprise the RGR. The RGR of the weed was less affected by the two competition levels than the RGR of either maize hybrid. When the cause of this behaviour is analysed, the small decrease in NAR appears to be the variable responsible for the maintenance of the RGR in the weed. Holt and Orcutt (1991) established a close relationship between the aggressiveness of weeds of the C₄ metabolic pathway and their NAR. A similar trend for the maintenance of NAR was found by Stuart *et al.* (1985), when *S. halepense* grew under conditions of water deficit, without competition. Nevertheless, the contribution of the parameters that comprise the RGR to the aggressiveness of weeds can change depending on the environmental conditions under which the competition is established and on the species under competition (Radosevich & Roush, 1990), which can modify the contribution of each growth parameter to the change of the RGR (Poorter, 1989).

In this study, the change in the RGR of *S. halepense* growing under water competition was due to a decrease of the aerial morphological growth components (LMF and SLA) and an increased allocation of biomass to the roots. This change in the distribution of above-ground biomass towards the roots may have allowed the maintenance of water extraction and thereby NAR during the competitive process. This trend is in agreement with data from Holt and Orcutt (1991), which associated the higher *S. halepense* aggressivity with the aptitude of the weed to support high rates of growth and net assimilation. Conversely, in maize, the change of the

RGR under competition for water was due to an adjustment in the physiological component (NAR). The distribution of assimilates towards the roots did not increase in maize in the same proportion as observed in *S. halepense*. Thus, under competition for water, both species of the plant association presented different growth strategies. Moreover, *S. halepense* showed an important root morphological plasticity, with an important increase in RLR which may have allowed *S. halepense* to maintain growth under conditions of severe competition for soil water. This difference in response is consistent with reports from Radosevich and Roush (1990), who determined that it is the responses of each species to the different environmental conditions that establish competitive hierarchies, and that these are not the product of constitutive characteristics (always present regardless of the levels of competition) of the species subject to competition.

Biomass allocation affected by the competitive process

As *S. halepense* grew in competition for soil water, it followed a trend similar to that described as 'functional equilibrium', increasing the fraction of root biomass. This behaviour coincides with that established by Poorter and Nagel (2000) and Shipley and Meziane (2002), who reported a proportional increase in the root fraction as soil water availability decreases. Shipley and Meziane (2002) determined that, in different species, this trend to the model 'functional equilibrium' takes place in

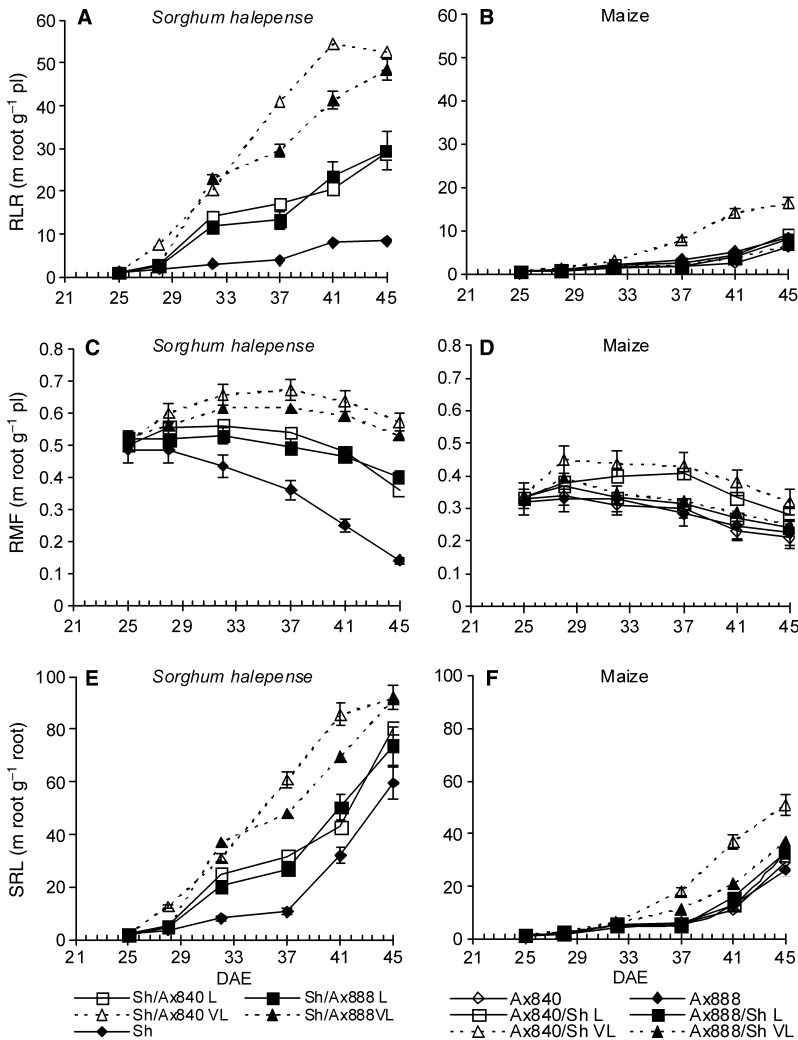


Fig. 3 Time course (days after emergence, DAE) of root length ratio (A, B: RLR, m root g⁻¹ pl), root mass fraction (C, D: RMF, g root g⁻¹ plant) and specific root length (E, F: SRL, m root g⁻¹ root) of *Sorghum halepense* (Sh) (A, C and E) and two hybrids of maize (Ax840, Ax888) (B, D and F) grown alone or in competition at two levels of water availability (low, L and very low, VL). Values were averaged over two growing seasons. Vertical bars indicate standard error (SE).

the short term, in the first 2 months of the growing cycle. Also, Cahill (2003) showed that plasticity in biomass allocation between root and aerial structures occurs in early stages of the growing cycle of species in competition, and that in this situation there is a trend for increased allocation of biomass to roots with increasing soil resource restrictions. The results obtained here become important because the competitive process between weeds and crops were recorded in the early weeks after crop emergence (Otto *et al.*, 2009).

Competition for soil water in *S. halepense* produced a significant decrease in biomass allocation to rhizomes. Despite maintaining a high RGR, competition with the two maize hybrids influenced the vegetative growth of the weed. Conversely, changes in root biomass of maize hybrids were much smaller than in *S. halepense*, and were non-significant under soil water competition. Similarly, a decrease of biomass allocated to rhizomes when *S. halepense* was subjected to intraspecific radiation competition was observed by Williams and Ingber (1977). In this case, the LMF was maintained through-

out the competitive process. Therefore, *S. halepense* tends to make an adjustment of similar magnitude in the production of leaves and rhizomes, allocating a greater proportion of biomass to the structures that are experiencing competition, i.e. roots. This behaviour was independent of the maize hybrid with which the weed competed.

Root growth and RGR

Sorghum halepense maintained the ability to grow in competition with maize through the maintenance of NAR during the evaluation period. This behaviour is the result of the dynamics of root growth in the weed at the two competition levels studied. The variation of root growth in *S. halepense* is in agreement with Konings *et al.* (1989), Eissenstat (1997) and Derner and Briske (1999), who showed a significant plasticity in weeds for a number of root variables. Konings *et al.* (1989) found that those species with a high NAR are characterised by high photosynthetic and transpiration rates. According

Fig. 4 Time course (days after emergence, DAE) of Very fine root length (VfRL, m root plant⁻¹) of *Sorghum halepense* (Sh) (A) and two hybrids of maize (Ax840, Ax888) (B) grown alone or in competition at two levels of water availability (low, L and very low, VL). Values were averaged over two growing seasons. Vertical bars indicate standard error (SE).

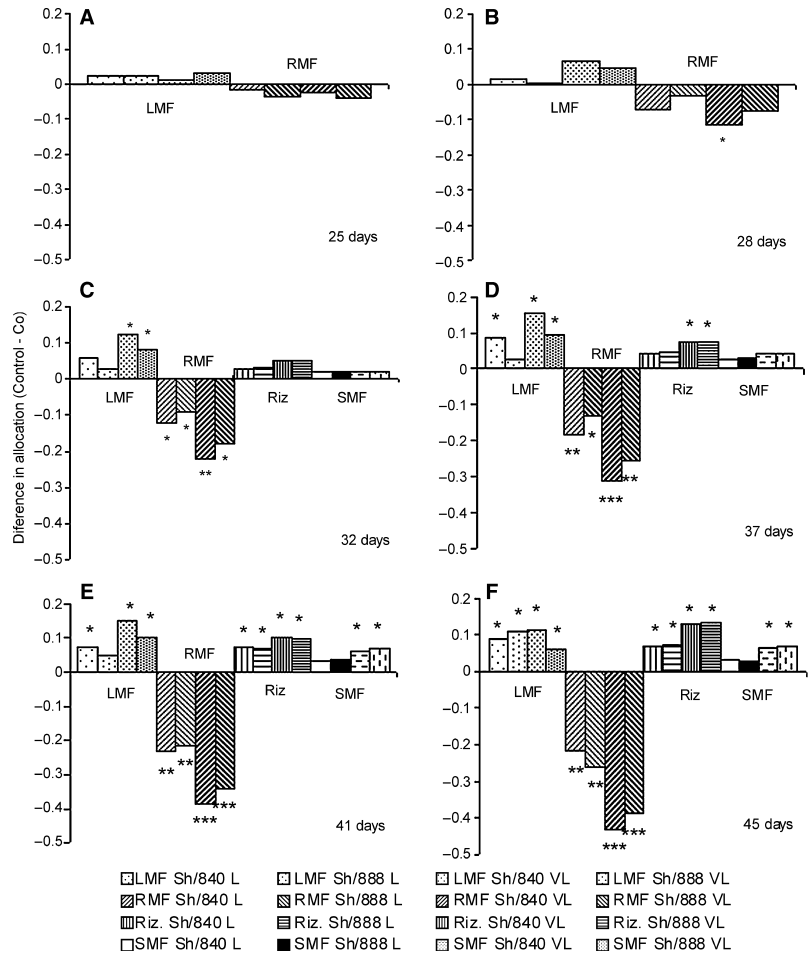
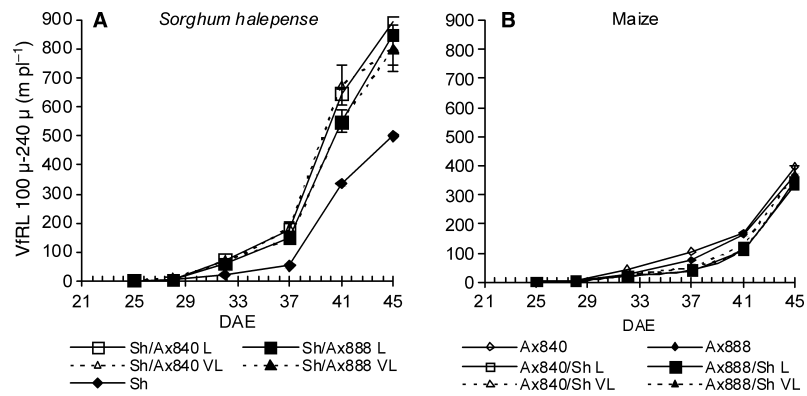


Fig. 5 Difference in biomass allocation in *Sorghum halepense* (Sh) at 25 (A), 28 (B), 32 (C), 37 (D), 41 (E) and 45 (F) days after emergence, between plants grown under competition (Co) at two levels of water availability (low, L and very low, VL) with respect to control treatment (Control, absence of competition). Asterisks at the bottom of the panels indicate the significance level under the H0 hypothesis of no difference in allocation. *P < 0.05; **P < 0.01; ***P < 0.001.

to this, these species require a larger root absorption capacity of soil resources, such capacity being associated with root biomass and root length. Moreover, Eissenstat (1997) stated that the roots of those species able to maximise the absorption of soil resources in the short term (one growing season), are characterised by a high rate of growth, smaller diameter and high rates of absorption of nutrients and water. *Sorghum halepense* increased the amount of biomass allocated to roots, the specific root length and the length of roots between

100 μm and 240 μm. Among the variables that compose the root length ratio, the SRL changed more than the RMF. *Sorghum halepense* reached a higher absorption capacity with respect to its transpiration area. Eissenstat (1997) stated that a greater root length, due to a greater RMF or SRL will promote the absorption of soil resources, thereby providing a greater competitive ability to species that possess these root characteristics. Thus, the higher root morphological plasticity of *S. halepense*, might have favoured the absorption of

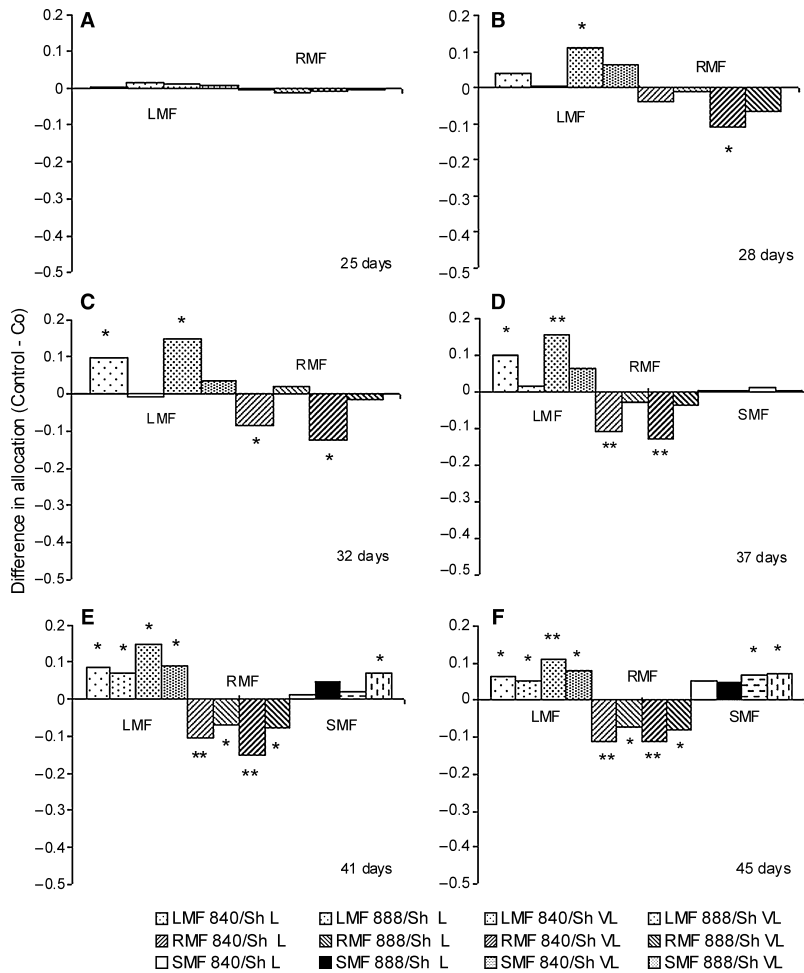


Fig. 6 Difference in biomass allocation in maize hybrids at different days after emergence at 25 (A), 28 (B), 32 (C), 37 (D), 41 (E) and 45 (F), between plants grown under competition (Co) at two levels of water availability (low, L and very low, VL) with respect to control treatment (Control, absence of competition). Asterisks at the bottom of the panels indicate the significance level under the H0 hypothesis of no difference in allocation. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

water during the competition, which may have helped to sustain NAR (Derner & Briske, 1999). However, the higher proportional allocation to roots with a greater length in *S. halepense* produced a significant reduction of rhizome biomass, which could adversely affect the reproductive strategy of the weed.

On the other hand, only the Ax840 hybrid showed some (albeit small) root growth plasticity, with a slight increase in the RMF and SRL under water competition. This was not associated with the formation of smaller diameter roots that would have helped to maintain the absorption capacity. Ryser (1998) shows that a higher RLR through a greater SRL allows crops to overcome the frequent fluctuations in availability of soil resources.

Plant competition studies are important for developing weed management strategies, as a result of a better understanding of the physiology of the interspecific competition between the weed and crop (Bridgemohan & McDavid, 1993). An understanding of the mechanisms underlying competitive interactions can only be achieved when the limiting factors and physiological responses to competition are identified. Our results show that soil water competition during the vegetative grow-

ing cycle of maize could lead to an intensive competitive process, dominated by *S. halepense* root growth and plasticity. The outcome of weed/crop competition for water or any other resource depends upon the relative abilities of weed and crop to obtain the resource and to tolerate a deficit of the resource (Patterson, 1995) and this outcome will be affected by partitioning of new biomass to above- and below-ground plant organs in response to water supply. According to our results, the potential use of competitive ability of maize in the design of an integrated *S. halepense* management programme will be severely limited. These results have clear consequences for the agronomic usefulness of competitive ability in maize management strategies to sustain crop yield at current levels.

Conclusions

Competition for soil moisture leads to a morphological adjustment (LAR) in the relative growth rate of *S. halepense*, while maintaining the NAR during the competitive process. In contrast, in maize, the decrease in relative growth rate was due to a decline in net

assimilation rate, with a differential response between the hybrids tested.

The increase in the root mass and root length in *S. halepense* probably contributes to maintain the rate of growth at the different levels of competition tested.

Sorghum halepense shows an adjustment in biomass allocation to leaves and rhizomes. This response is independent of the maize hybrid with which *S. halepense* competes.

Maize hybrids showed less root plasticity than *S. halepense*. An increase in root mass fraction and specific root length was only observed in Ax840, a hybrid adapted to limiting soil conditions, but this increase was half of that observed in *S. halepense*.

There was no formation of fine roots to maintain maize water absorption during competition in any of the hybrids tested. According to this, the competitive process could be dominated by *S. halepense*.

The greater increase both in biomass partitioned to roots and root length by *S. halepense* might negatively impact maize ability to compete for water during the crop critical competition period.

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