Early responses to high crop population density in sunflower: Controls and effects of the crop self-organization process

Mónica López Pereira[1], Nora Trápani[2], Jorge Casal[2], Antonio Hall[2]

[1]Cátedra de Cultivos Industriales. Facultad de Agronomía. Universidad de Buenos Aires, Argentina, E-mail: pereiram@mail.agro.uba.ar,

[2]IFEVA, CONICET/ Facultad de Agronomía. Universidad de Buenos Aires, Avda. San Martín 4453 (1417) Buenos Aires, Argentina, E-mail: trapani@ifeva.edu.ar; casal@ifeva.edu.ar, hall@ifeva.edu.ar

ABSTRACT

Plants in the rows of high crop population density sunflower crops exhibit a self-organizing process that commences shortly after seedling emergence: a given stem inclines towards one inter-row and the neighbouring stem inclines towards the opposite inter-row. To date, the causes and consequences of this process have not been explored in sunflower or in other grain crops. The aim of this work was to describe the dynamics of sunflower self-organization, focusing on the causes that elicit this crop response. Five experiments were conducted at the Facultad de Agronomía, Universidad de Buenos Aires. Factors affecting crop responses that were examined included: crop population density, quality of light incident on upper leaves of the plants, and the mechanical restriction of the self-organization process. Dynamics of the process were followed at four-day intervals or, in a more detailed fashion, using time-lapse photography to document the organization process and the degree of shading between neighbouring plants at 10-minute intervals. Effects of self-organization on grain yield and grain number were determined in some experiments. The self organization process (as exhibited by the proportion, of all plants in a row, of inclined stems) was greater and occurred earlier in the high population density plots. Thus, 70% of plants deviated from the vertical position at 14 pl. m^{-2} (equally distributed among the two inter-row positions) at floral initiation as against 0% at 5 pl. m^{-2}. Low red/far red ratio light (but not low blue light) incident on the upper portion of otherwise unshaded plants induced a high incidence of stem inclination (82%) and greater inclination angles (30º) than in the controls (0%, 0º). Analysis of time-lapse photography records for individual plants showed that the initiation of stem inclination took place shortly after the plant began to be shaded by its neighbours. Grain yield was significantly lower in plots in which the self-organization process was mechanically restricted. It is concluded that a) shading of the target plant by the leaves of neighbouring plants reduced the red/far red ratio of the light incident on the target plant, inducing stem inclination; b) stem inclination diminished the negative effects of the increased crop density on grain number and grain yield per plant.

Key words: crop density – light influence – radiation interception – self organization –stem inclination.

INTRODUCTION

Under non-limiting conditions, sunflower crop yield responds positively to increases in plant population density above those usual (ca. 5 pl.m^{-2}) in commercial production in Argentina (López Pereira et al., 2004a). The effects of increased crop population density involve changes in light quality within the canopy. Plants can perceive changes in light quality (i.e. proportion of red/far red, blue light) and respond by exhibiting modifications in morphological and physiological attributes during the early stages of crop development (Ballaré et al., 1987). For example, at the bud visible stage, sunflower basal internodes became longer and heavier as crop population density increased (2 to 14 plants m^{-2}) (López Pereira et al., 2004b). De la Vega and Hall (pers. comm. 2002) observed that in denser stands (>5 plants m^{-2}) the plants within a row adopt a regular arrangement: one stem inclines towards one inter-row and the neighbouring stem inclines towards the opposite inter-row, and at physiological maturity this pattern is evident along the whole of the row. Preliminary experiments have demonstrated that this alternating inclination of stems along the row could not arise by chance (López Pereira et al., 2004b). This self-organization process within a given row might increase radiation interception and aerial biomass production in early crop development phases, and possibly affect yield.

While the movement of leaves (Lang and Begg, 1979; Casal and Sadras, 1987) and stems (Buda, 2003) has been widely studied in sunflower, there are no reports of self-organization responses to increments in crop population density, either in sunflower or in other grain crops. The aims of this work were: i) to describe the dynamics of the process of stem inclination in early stages of crop development; ii) to determine which of the possible light quality signals known to be involved in plant-to-plant

communication (red/far red light [R/FR] ratio and /or blue light [B]) are involved in this process; and iii) to evaluate the effects of stem inclination on yield and generation of reproduction structures.

MATERIALS AND METHODS

Five experiments were conducted at the experimental field of the Facultad de Agronomía, Universidad de Buenos Aires (34º35 ´ S., 58th 29'W.) to achieve the objectives indicated above. The plots were fertilized (60 kg N ha^{-1}) and irrigated, and diseases, insects and lodging controlled. Crops were over-sown and desired crop population densities were established by removing plants at the two-leaf stage. The distance between rows was 0.70 m. The same hybrid (Paraíso 20) was sown in all experiments. Details of the experiments are provided below.

i) Dynamics of the self-organization process

Two experiments were conducted; *Experiment 1*: 2003-04. The experiment was laid out in a randomised complete block design with three replications. Crop population densities covered a broad range of densities (0.2 to 14.3 plants m^{-2}). Crop rows were oriented N-S and number of inclined stems for 40 contiguous plants in a row and their inter-row orientation (E or W) was evaluated every fourth day from 20 days after crop emergence (dae) until the bud visible stage. *Experiment 2*: 2005-2006. In this experiment time-lapse photography was used to generate a more detailed record of the self-organization process. Plants were sown at a very high crop population density (20 plants m^{-2}), and a system of web-cams and a CPU were devised which allowed plant position to be registered every 10 minutes. Three cameras, each focused on a section of row, were supported on a framework above a 1-m length of row. The images were analyzed using JPG video version 1.05.0.0-freeware. To simplify the analysis, the total image data base was segmented, and apex position (distance from the row axis) and proportion (with respect to total) of leaf area per plant shaded by neighbouring plants were quantified at 9, 11, 13, 15 and 18 hrs of each day, beginning 8 dae, when mutual shading between neighbours and deviation of the plant apex from the vertical started to become evident, and continued up to 23 dae. A daily integral of the fractional shaded area per plant was synthesized from the five daily observations. Shading was computed up to about 280 hours from the start of imaging (at later stages of the process this became too difficult) but apex position was documented for a further 50 hours.

ii) Controls of stem inclination: light signals

In *Experiment 3* (2004), the quality of light incident on the upper leaves of the plants was manipulated using filters that absorbed or reflected solar light in different wavelengths, generating: i) a low R/FR ratio; ii) a normal (sunlight) R/FR ratio (i.e., control), and iii) a low blue irradiance. The filters (0.08 m x 0.08 m) were centred over the apices of ten plants per treatment. Plots were sown at a low crop population density (5 plants m^{-2}) so that light quality impinging on the apex and leaves of the target plant were not affected by the leaves of the nearby plants. At 96 hours after the beginning of the first day in which filters were put in place, the number of treated plants that had stems which deviated from the vertical were registered and the angle of stem inclination (with respect to the vertical) measured.

iii) Effects of stem inclination

During the 2004-05 (*Experiment 4*) and 2005-06 (*Experiment 5*) seasons experiments using high crop population densities (10 and 14 plants m^{-2}) were conducted. A randomized complete block design was used, with two factors (crop density, self-organization [natural vs. none, in which stems were forcibly restrained in the vertical position using guide-wires] and three replicates per treatment. At physiological maturity, yield and total grain number were determined on a sample of 30 plants per treatment.

RESULTS

In Experiment 1, the self-organization process began early (before 27 dae) at 14 pl.m^{-2}, while at 5 pl.m^{-2} very few plants had deviated from the vertical at 49 dae (Fig. 1). The process was gradual, with increasing proportions of plants showing inclination, so that almost all stems in the 14 pl.m^{-2} plots were inclined at 49 dae, with almost equal proportions in the E and W inter-rows. Although not shown in Fig. 1, the final pattern was regular, with neighbouring plants inclining toward opposite inter-rows. The small proportion of plants not showing inclination at 49 dae in the 14 pl.m^{-2} plots were usually suppressed (little growth) by their neighbours. Interestingly, the process began in different sectors of the row, in patches, and some degree of "re-orientation" was involved as patches began to overlap. At the beginning of the process, the

proportion of stems inclining towards the E was higher than the proportion of stems inclined towards the W. At the end of the process, the proportion of stems inclined towards each inter-row became similar because the proportion of plants inclined towards the W increased. At the highest crop population density (14 plants m^{-2}), the stem inclination process began 15-20 dae, before the beginning of floral initiation. A large ($\approx$70%) proportion of the stems showed inclination at the time when floral initiation was completed in these plots (Fig. 1).
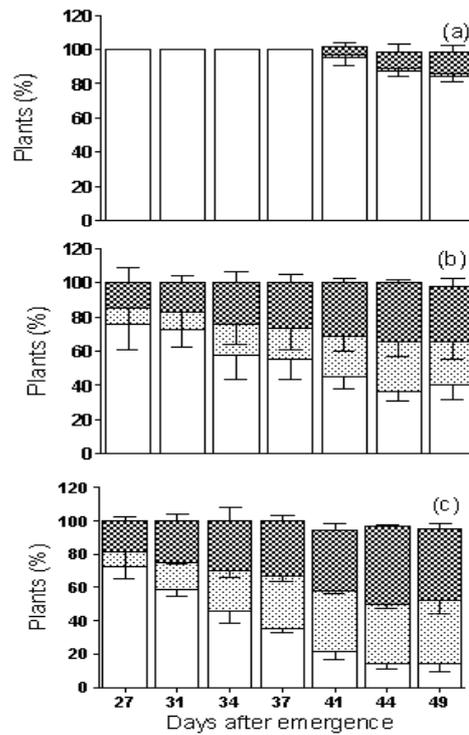

Fig. 1. Dynamics of stem inclination from 20 days after emergence to bud visible in crops sown at three crop population densities: a) 5 plants m^{-2}, b) 10 plants m^{-2}, and c) 14 plants m^{-2}. Each bar represents the proportion of plants not inclined (white), inclined towards the E (heavy stippling) and towards the W (light stippling). The line below panel c) represents the duration of the floral initiation period in these crops. The vertical lines on the bars indicate ± a standard error, n= 3 (40 plants per replication). Experiment 1.

In Experiment 2, stem inclination began shortly after neighbouring plants began to be shaded by their neighbours (Fig. 2), with the shaded plant inclining away from the row axis towards the inter-row space. The plants that first experienced shading were the first to show this response (e.g., Plants 1 and 2 vs. Plant 3, Fig. 2). The effects found in the 14 remaining plants evaluated in this experiment (data not shown) were consistent with those illustrated for the three plants shown in Fig. 2.
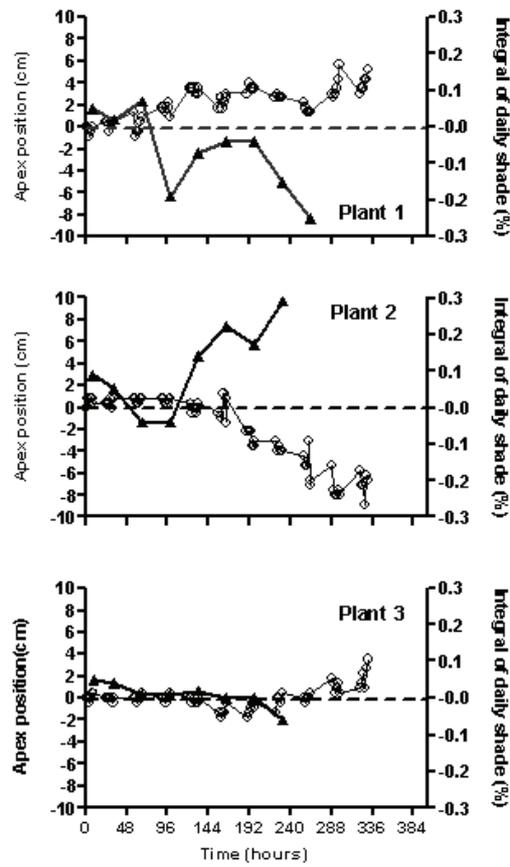
Fig. 2. Dynamics of the apex position (cm from row axis, circles, five observations per day) and daily shade integral (mean daily fraction of total plant leaf area, triangles) for three plants growing in plots sown at 20 plants m^{-2}. The dashed horizontal line indicates the row axis. The negative and positive values represent the two inter-rows, and are used to show the position where the shading took place and position of the plant apex. Daily shade integral estimates were not made after about 280 hours after the start of observations (8 dae) because the degree of plant-to-plant interference became too difficult to resolve in the two-dimensional images.

In Experiment 3, proportion of inclined plants and the angle of stem inclination evoked by low R/FR incident on the upper leaves were greater than in the other two treatments (little response in low blue light treatment and insignificant for the control (neutral filter) treatment) (Fig. 3). Clearly, light of a low R/FR ratio incident on the leaves can evoke stem inclination. The R/FR ratio measured below the upper leaves close to the row axis was 0.55±0.12, in contrast to 1.17±0.07 above the upper leaves close to the inter-rows. These values are consistent with those obtained using the R/FR filters.
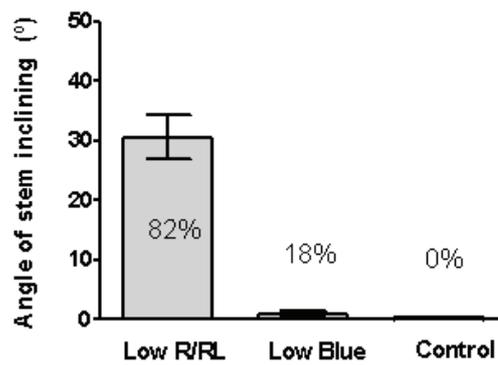
Fig. 3. Effects of light of low red/far red (R/FR) ratio, low blue (B) and normal (sunlight) R/FR and blue (control) on the angle of inclination of sunflower stems. The numerical values on or above each column indicate the proportion (%) of inclined plants (n=10) in each treatment. The vertical lines on the bars indicate ± a standard error. Experiment 3.

In Experiments 4 and 5, grain yield was significantly (Exp.4 p≤0.03, Exp.5 p≤0.01) lower in plots in which stem inclination was forcibly restricted (Exp.5 = 25.2 ±1.5; Exp. 6 =16.9 ± 1.8 g per plant) than in plots in which the natural self-organization was allowed (Exp.5 = 30.6 ±0.7; Exp. 6 =31.4 ±0.7 g per plant). These effects on grain yield were associated with significant reductions in grain number per plant in both experiments (Exp.4 p≤0.01; Exp.5 p≤0.01).

DISCUSSION

Our results indicate that the process of crop self-organization is an important response of sunflower crop to high crop population densities. This process occurs over time, is hastened at high crop population densities and the propagation of the pattern occurs in patches. Mutual shading between leaves of neighbouring plants (briefly) precedes the deviation of the stems from the vertical. The fact that low R/FR ratios in the light incident on the upper leaves can evoke stem inclination is consistent with the reduction in R/FR ratio of light transmitted through green leaves. The weak response to low blue light of the process (light transmitted through leaves is depleted in blue) suggests that phytochromes rather than cryptochromes or phototropins are the photoreceptors involved. This is the first time that it has been shown that the quality of light impinging on leaves can alter stem position (previous reports in other species involve detection/response associations limited to either leaves (Maddoni et al., 2002) or stems (Ballaré et al., 1991) The process would appear to have an effect on crop yield. It remains to be established whether the effect on crop yield is mediated by changes in resource capture (e.g., higher fractional interception); resource allocation (e.g., less competition for biomass between stem and floral structures); direct photomorphogenic effects (e.g., in soybean, the abscission of reproductive structures in the lower strata of the canopy during flowering was lower in plots with high R/FR; Heindel and Brun, 1983); or a combination of these effects.

Another issue arising from the identification of this process relates to possible intra-specific variability for the intensity of this process (and we have preliminary evidence to support this possibility). In Argentina, there is some interest in intersown sunflower/soybean crops. An important issue here is the conditions for soybean seedling establishment and early growth in the space between the rows of sunflower. Sunflower hybrids less sensitive to signals produced by neighbouring plants might produce less shade for the soybean intercrop. By contrast, in non-uniform stands of pure sunflower crops (a common circumstance in sunflower crops in Argentina), it would be desirable to have cultivars capable of responding to environmental heterogeneity and ensuring greater resource capture.

ACKNOWLEDGEMENTS

REFERENCES

Ballaré, C.L., R.A. Sánchez, A.L. Scopel, J.J. Casal, and C.M. Ghersa. 1987. Early detection of neighbour plants by phytochrome perception of spectral changes in reflected sunlight. Plant Cell Environ. 10:551-557.

Ballaré, C.L., A.L. Scopel, and R.A. Sánchez. 1991. Photocontrol of stem elongation in plant neighbourhoods: effects of photon fluence rate under natural conditions of radiation. Plant Cell Environ. 14:57-65.

Buda, A., T. Zawadzki, M. Krupa, M. Stolarz, and W. Okioski. 2003. Daily and infradian rhythms of circumnutation intensity in *Helianthus annuus*. Physiol. Plant. 119:582-589.

Cantagallo, J.E., and A.J. Hall. 2002. Seed number in sunflower as affected by light stress during the floret differentiation interval. Field Crops Res., 74:173-181.

Casal, J., and V. Sadras. 1987. Effects of end-of-day red/far red ratio on growth and orientation of sunflower leaves. Bot. Gaz. 148:463-467.

Heindel, J.C., and W.A. Brun. 1983. Light and shade effects on abscission and 14C photoassimilate partitioning among reproductive structures in soybean. Plant Physiol. 73:434-439.

Lang, A., and J. Begg. 1979. Movements of. *Helianthus. annuus* leaves and heads. J. Appl. Ecol. 16:299-305.

López Pereira, M., N. Trápani, G. Piñeiro, and A.J. Hall. 2004a. Responses of sunflower to stand structure and crop population density: effects on leaf area and yield. p. 315-321 (vol. 1). In: Proc. 16th Int. Sunflower Conf., Fargo, ND.

López Pereira, M., N. Trápani, J. Casal, and A. Hall. 2004b. La inclinación ordenada de tallos en el cultivo de girasol a alta densidad. p. 80. In: XXV Reunión Argentina de Fisiologia Vegetal.

Maddoni, G., M.E. Otegui, B. Andrieu, M. Chelle, and J. Casal. 2002. Maize leaves turn away from neighbords. Plant Physiol. 130:1181-1189.