Annals of Botany **85**: 187–195, 2000
doi: 10.1006/anbo.1999.1013, available online at http://www.idealibrary.com on IDEAL®

Profiles of Leaf Senescence During Reproductive Growth of Sunflower and Maize

V. O. SADRAS*, L. ECHARTE and F. H. ANDRADE

Universidad de Mar del Plata-INTA Balcarce, CC 276, Balcarce 7620, Argentina

Received: 5 July 1999 Returned for revision: 2 September 1999 Accepted: 4 October 1999

We investigated the effect of reproductive growth on the profiles of leaf senescence in maize (*Zea mays* L.) and sunflower (*Helianthus annuus* L.). Leaf senescence after flowering was assessed using both structural (leaf chlorophyll, nitrogen and dry matter) and functional (photosynthesis) variables in undisturbed plants (+G) and in plants in which grain set was prevented (−G). Two weeks after flowering, lack of grain accelerated senescence in maize and delayed senescence in sunflower as indicated by leaf chlorophyll; leaf nitrogen and dry matter were less sensitive response variables. Lack of interaction between reproductive treatment and leaf position indicates that the senescence signal, whatever its nature, was equally effective throughout the plant in both species. In both species, feedback inhibition of photosynthesis was first detected 30–35 d after flowering; excess carbohydrate in the leaves was therefore an unlikely trigger of accelerated senescence in maize. As reproductive development progressed, differences between +G and −G plants were more marked in sunflower, and tended to disappear or reverse in maize. In sunflower, interactions between leaf position and reproductive treatment—attributable to the local effect of grain—were detected around 20–27 d after flowering.

Key words: *Helianthus annuus*, *Zea mays*, chlorophyll, light, nitrogen, photosynthesis, reproductive growth, senescence, source-sink, SPAD.

INTRODUCTION

Sunflower (*Helianthus annuus* L.) oil yield is closely related to the duration of leaf area from anthesis to maturity (Hall *et al*., 1985; Merrien and Grandin, 1990). Duration of leaf area during grain growth also accounts for a large proportion of the variation in the yield of maize (*Zea mays* L.) grown under contrasting supplies of water and nitrogen (Wolfe *et al*., 1988*a*).

Duration of leaf area between anthesis and maturity can be analysed as a function of two variables: leaf area at anthesis and rate of leaf senescence during grain filling. A number of environmental and plant factors affect the onset and/or rate of leaf senescence. Among the plant factors, reproductive growth has a recognized influence on leaf senescence. Experiments in which grain set was prevented demonstrated a consistent delay and/or slowing down of leaf senescence in oilseed species including soybean [*Glycine max* (L.) Merrill] and sunflower (Lindoo and Noodén, 1977; Ho *et al*. 1987; Ho and Below, 1989). Owing to intraspecific variation, the relation between reproductive growth of cereals and leaf senescence is ambiguous. In maize, ear removal may delay or accelerate leaf senescence (Thomas and Smart, 1993). According to Crafts-Brandner and Poneleit (1987), both delayed and rapid senescence in maize are dominant traits transmissible to F_1 hybrids.

We used both structural (leaf dry matter, chlorophyll and nitrogen content) and functional (photosynthesis) variables to characterize the pattern of leaf senescence after flowering in undisturbed plants (+G) and in plants in which grain set was prevented (−G). Our approach had three main components. Firstly, we compared sunflower and maize—species with putatively contrasting responses. Comparative physiology is a powerful tool (Andrade, 1995; Lu and Neumann, 1998). Secondly, we characterized the vertical profile of leaves, in contrast to experiments focusing on individual leaves or whole plants. Studies of profiles have contributed to elucidation of local effects of sinks on leaf senescence (Wolfe *et al*., 1988*b*; Sadras *et al*., 1993). Thirdly, we included +G and −G plants in the same crop, in contrast with the more common arrangement of treatments in separate plots. If manipulation of grain set affects the pattern of leaf senescence, the light profile in 'pure' +G and −G stands might diverge. Owing to the strong influence of light on leaf senescence (Rousseaux *et al*., 1993), differences in light profiles triggered by differential senescence—initially caused by manipulation of reproductive growth—may feed-back on senescence processes. By alternating +G and −G plants in the same crop, and by measuring light profiles for individual plants, we attempted to separate direct effects of grain from the indirect effects associated with changes in the profile of light.

MATERIALS AND METHODS

Crops

Maize ('Dekalb 664') was sown on 6 Oct. 1998 and sunflower ('CF11') on 20 Oct. 1998 on a deep Typic Argiudol at Balcarce, Argentina (37° S, 58° W). Plots were fertilized with 20 kg P ha^{-1} and 140 kg N ha^{-1}. Space between rows was 0·7 m in both crops and plant population densities were eight plants m^{-2} in maize and five plants m^{-2} in sunflower. Both crops were irrigated to replenish the soil

* For correspondence. E-mail vsadras@balcarce.inta.gov.ar

0305-7364/00/020187+09 $35.00/0

profile at flowering; rainfall during the period of grain growth (55 mm) was complemented with irrigation to ensure good water supply. Weeds were controlled both with herbicides (2 l atrazine ha^{-1} + 6·4 l butylate ha^{-1} in maize; 0·5 l flurochloridone ha^{-1} + 2 l metolachlor ha^{-1} in sunflower) and manually during the early stages of crop growth.

Treatments

Maize and sunflower crops were grown in different sections of the same field; no attempt was made to include both species into a common layout because of practical issues of weed management and herbicide use. Four maize plots (each including eight rows by 12 m) and four sunflower plots (each of four rows by 30 m) were established. Two treatments were assigned alternately to the plants in the central rows of each plot: plants with (+G) and without grain (−G). In sunflower, −G plants had their heads removed at anthesis. To avoid leaf damage associated with ear removal in maize, we covered the ears of −G plants with bags to prevent pollination and grain set.

Measurements and observations

Phenological observations were made twice weekly to determine the time of anthesis in sunflower and the time of silking in maize. These stages are referred to as 'flowering' hereafter. At flowering, light profiles were measured on the basis of (*a*) individual leaves, with a quantum sensor (LI-COR, Lincoln, Nebraska, USA) and (*b*) the whole canopy, with a line quantum sensor (LI-COR 191 SB). Measurements at the canopy level provided a reference for the light profiles measured at the leaf level, which were regarded as less reliable due to sunflecks. Light profiles at the leaf level were measured 4 weeks after flowering to compare the light profiles of individual +G and −G plants.

Profiles of leaf chlorophyll were measured weekly with a SPAD-502 meter (Minolta, Plainfield, Illinois, USA). For each replicate and treatment, every second leaf from three plants was measured; three readings per leaf were averaged to account for within-leaf variation (Drouet and Bonhomme, 1999). Rousseaux (1997) reported a strong linear relation between SPAD measurements and laboratory determinations of sunflower leaf chlorophyll (Inskeep and Bloom, 1985) within a range of SPAD units from 20 to 45. Four times during the experimental period we sampled every second leaf lamina from three plants per replicate and treatment to measure dry matter and nitrogen content. Leaf dry matter was determined after oven drying to constant weight, and nitrogen content of milled samples was quantified using the method of Nelson and Sommers (1973). Leaves tend to shrink and became brittle as senescence proceeds, making area measurements less accurate than weighing. Thus nitrogen content was calculated on a dry matter basis (LNC, %); comparisons with nitrogen content per unit leaf area (SLN, g N m^{-2} leaf) are presented when appropriate. Four times during the experimental period we measured photosynthetic rate of leaves at three positions in one or two plants per replicate and treatment. Measurements on leaves exposed to full sunlight were taken at solar noon ± 1 h using a portable photosynthesis system LI-COR 6200 (LI-COR, Lincoln, Nebraska, USA).

For each measurement date and response variable, ANOVA was used to assess the effect of reproductive treatment (+G *vs.* −G), leaf position (node), and leaf position × treatment interaction.

RESULTS

Phenology

Flowering time was 8 January for maize (94 d after sowing, DAS) and 7 January for sunflower (79 DAS). Plants of both species were therefore exposed to similar light and temperature regimes during the period of grain set and growth (Table 1).

Light profile

At flowering, the fraction of incident PAR decreased almost linearly with node number in both sunflower and maize (Fig. 1A and D). These light profiles, measured with a quantum sensor at the leaf level, were consistent with the canopy profiles characterized with a linear sensor (Fig. 1B and E). In both species the regression between these variables was highly significant: $r^2 = 0{\cdot}96$, $P < 0{\cdot}003$ in sunflower; $r^2 = 0{\cdot}91$, $P < 0{\cdot}0009$ in maize. Both regressions had slopes not different from one, and intercepts not different from zero ($P > 0{\cdot}05$). Measurements at the leaf level were thus fairly reliable (Fig. 1B and E).

During grain growth, more light reached mid-position leaves in intact sunflower plants than in their decapitated counterparts ($P < 0{\cdot}002$) (Fig. 1C). This was because stems of intact plants bent due to the head weight, while stems of decapitated plants remained erect. In maize, reproductive treatment had no effect on the profile of light ($P > 0{\cdot}40$); the interaction between treatment and leaf position was also not significant ($P > 0{\cdot}54$) (Fig. 1F).

Leaf dry matter

At flowering, sunflower had 19 green leaves and maize 13. The main ear of maize was at the 6th node. Sunflower leaf dry matter increased linearly from the youngest leaf at the top of the plant to a broad maximum at nodes 11 to 15; leaves below the 15th node were slightly lighter than those at nodes 11 to 15 (Fig. 2). In maize, maximum dry matter corresponded to leaves around the ear node with markedly lighter leaves above and below this node (Fig. 2).

Two weeks after flowering, leaves in decapitated sunflower were heavier than in their intact counterparts; the opposite was true for maize (Fig. 2). Interaction between leaf position and treatment was not significant for either sunflower ($P > 0{\cdot}99$) or maize ($P > 0{\cdot}76$). Plots of the ratio between leaf dry matter 2 weeks after flowering and leaf dry matter at flowering help to interpret these responses (Fig. 2, insets). During the 2-week period after flowering, leaf dry matter in intact sunflower increased for nodes one to three, and did not change for nodes five to 19, i.e. ratio ≈ 1. In decapitated plants dry matter increased in all leaf positions, particularly in young leaves. In intact maize, all leaves accumulated dry matter during the 2 weeks after flowering; the gain was

TABLE 1. *Solar radiation, maximum and minimum air temperature during the period of grain set and growth*

Week after flowering	Maximum temperature (°C)	Minimum temperature (°C)	Radiation (MJ m^{-2} d^{-1})
1	23·3	9·7	24·5
2	31·0	15·0	21·7
3	26·4	15·8	20·8
4	25·6	11·7	21·4
5	27·6	10·8	23·8
6	26·5	12·8	20·2
7	30·3	16·5	16·6

Values are averages for the indicated weekly periods.

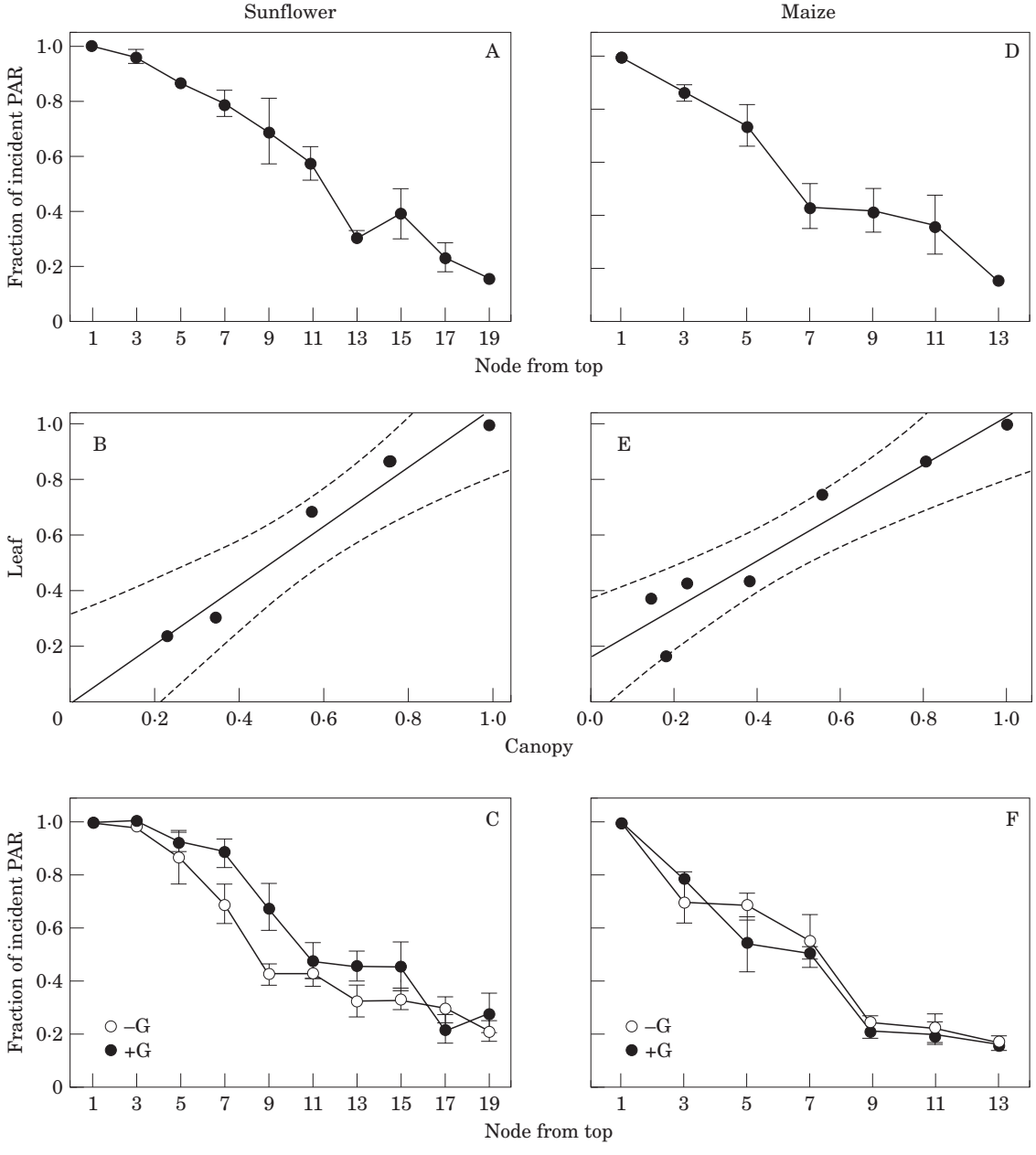

FIG. 1. Light profiles of sunflower and maize at flowering (A, B, D, E) and 4 weeks after flowering (C, F). Fraction of incident PAR measured at the leaf level with a quantum sensor (A, D). Fraction of incident PAR at the *leaf* level compared with the fraction of incident PAR measured with a linear sensor at the *canopy* level (B, E). Fraction of incident PAR measured at the leaf level 4 weeks after flowering (C, F). Bars are 2 s.e.m. Lines in B and E are the fitted linear regressions and the 95% confidence bands.

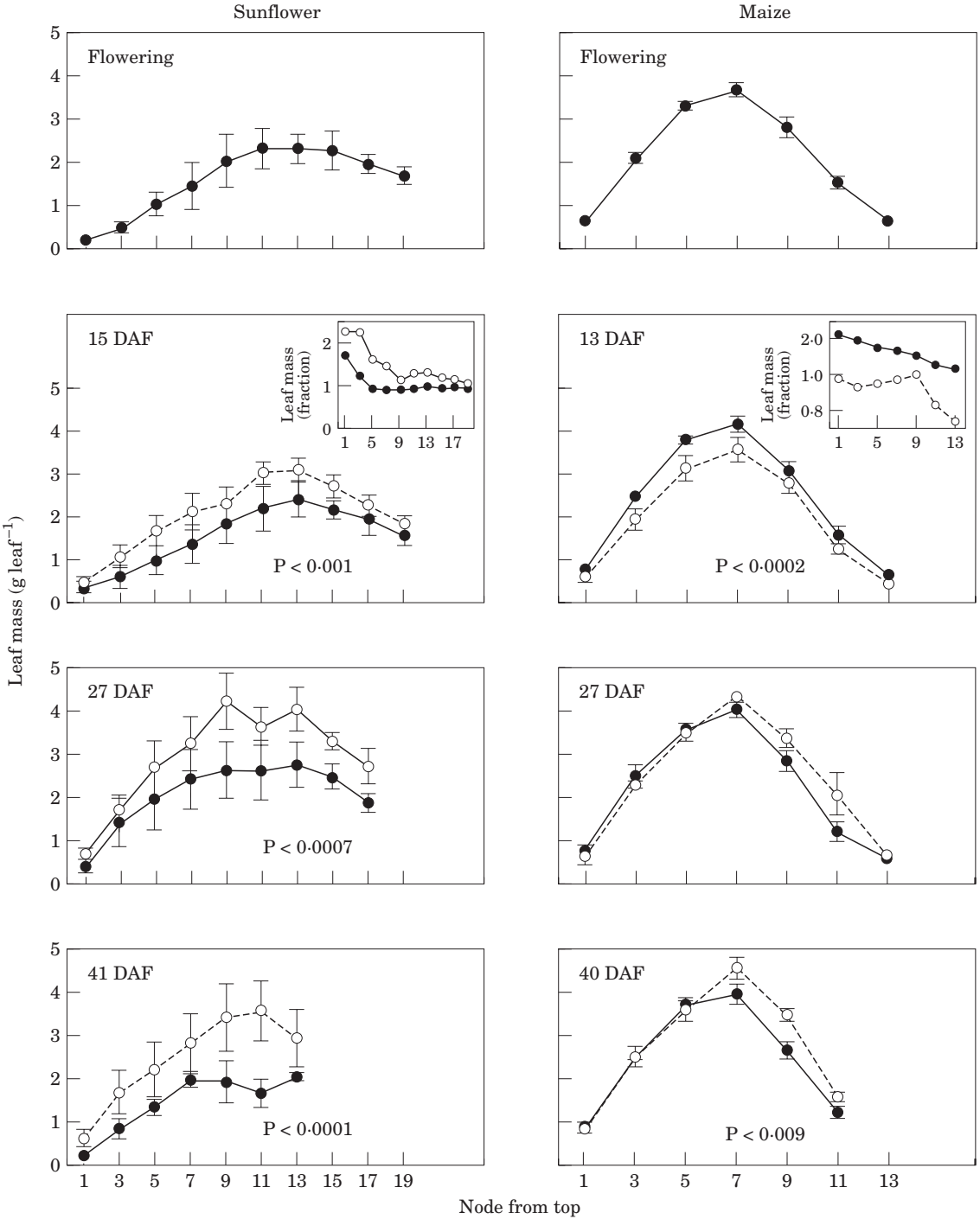

FIG. 2. Effect of reproductive growth on the profiles of leaf mass in sunflower and maize. Insets show leaf mass at 15 (sunflower) and 13 DAF (maize) as a fraction of the mass measured at flowering. *P* values indicate treatment effects. ○, −G; ●, +G. Bars are 2 s.e.m.

inversely proportional to leaf age. In contrast, leaf dry matter in plants with no grain did not change for nodes one to 9, and decreased for leaves below the 9th node.

As development progressed, treatment effects remained or increased in sunflower (27 and 41 d after flowering, DAF, Fig. 2). In contrast, the effect of treatment observed in maize 2 weeks after flowering tended to reverse: no effect was detected 27 DAF, and leaves were heavier in −G plants than in +G plants 40 DAF, in particular below the ear node (treatment × leaf position interaction: $P = 0{\cdot}057$) (Fig. 2).

Leaf chlorophyll

At flowering, leaf chlorophyll in sunflower increased linearly from the youngest leaf to the leaves in nodes nine to 15. In maize, maximum chlorophyll content was for leaves

in nodes seven to 11. In both species chlorophyll content of the older green leaves was slightly below the maximum (Fig. 3). Two weeks after flowering, chlorophyll content in leaves of decapitated sunflower was greater than in leaves of intact plants (Fig. 3). Conversely, chlorophyll content was less in leaves of −G maize than in their intact counterparts (Fig. 3). Interaction between leaf position and treatment was not significant for either sunflower ($P > 0{\cdot}92$) or maize ($P > 0{\cdot}11$).

As development progressed, differences between treatments diminished in both species. A significant interaction between treatment and leaf position was detected in sunflower at 20 DAF, i.e. the difference in chlorophyll between +G and −G plants was more marked in top and bottom leaves and less between nodes 5 and 13 ($P < 0{\cdot}0038$). As a consequence of this interaction, the profile flattened in sunflower more than in maize.

Leaf nitrogen

At flowering, profiles of LNC (Fig. 4) and SLN (not shown) both showed clear peaks at the 9th node in sunflower, and broad maxima around the ear node in maize. Two weeks after flowering, the profiles of LNC in intact plants did not differ from those of their −G counterparts in either species (Fig. 4). In sunflower, however, SLN was greater in decapitated than in intact plants (Fig. 4, inset). At 27 DAF, the effect of reproductive treatment was evident in both species (Fig. 4). Decapitated sunflower had greater LNC than intact plants particularly at top and bottom nodes (leaf position × treatment interaction: $P < 0{\cdot}05$). In maize, intact plants had greater LNC than their −G counterparts irrespective of leaf position (leaf position × treatment interaction: $P > 0{\cdot}28$). At 40–41 DAF, the difference between +G and −G plants established at 27 DAF was more marked in sunflower and attenuated in maize (Fig. 4).

Photosynthetic rate

In sunflower, the effect of treatment on photosynthesis was not significant at 14 and 26 DAF ($P > 0{\cdot}46$). The first effect of treatment was detected at 35 DAF when photosynthetic rate in leaves of intact plants was around 20 mmol m^{-2} s^{-1}. Lack of grain reduced photosynthetic rate by half in all leaf positions (treatment × leaf position interaction: $P > 0{\cdot}55$) (Fig. 5). A week later (41 DAF), photosynthetic rate in leaves of intact plants dropped to around 10 mmol m^{-2} s^{-1} and treatment effect was no longer evident in any leaf position (treatment: $P > 0{\cdot}58$; treatment × leaf position interaction: $P > 0{\cdot}45$).

In maize, effect of treatment was not significant at 13 and 26 DAF ($P > 0{\cdot}29$). At 30 and 38 DAF, lack of grain reduced photosynthetic rate (Fig. 5); the effect was similar at all leaf positions (treatment × leaf position interaction: $P > 0{\cdot}22$).

DISCUSSION

Manipulation of sowing date allowed maize and sunflower to grow under similar temperature regimes during the period of grain set and filling. We cannot ignore the fact that differential responses between species could have derived, to some extent, from the way in which −G treatments were established, i.e. head removal in sunflower *vs.* prevented pollination in maize. The responses found in this study, nonetheless, are consistent with those previously reported for maize and sunflower (Crafts-Brandner and Poneleit, 1987; Ho *et al.*, 1987; Ho and Below, 1989). Moreover, studies with soybean showed that the relation between leaf senescence and reproductive growth is consistent for a range of contrasting treatments including physical restriction and surgical removal of fruit (Miceli *et al.*, 1995).

Owing to the inclusion of both treatments in the same stand, light profiles of intact maize were similar to those of their −G counterparts (Fig. 1F). The difference in senescence between +G and −G maize was, therefore, unrelated to light. In contrast, owing to the bending of the stem, mid-position leaves received more light in intact sunflower than in their decapitated counterparts (Fig. 1C). Because low light intensity accelerates leaf senescence (Rousseaux *et al.*, 1993), differences in light profiles might have contributed to the significant interaction between treatment and leaf position measured at 20–27 DAF: lack of grain delayed senescence in leaves at the top and bottom of the plant, but not in intermediate positions (Figs 2 and 4). With the exception of this putative effect of light—that may have partially counteracted the effect of reproductive treatment—sunflower showed a consistent delay of leaf senescence attributable to lack of grain. This is consistent with previous studies showing: (1) that reproductive growth overrides light effects on the profile of sunflower leaf senescence; and (2) a local effect of the head that contributes to the fast senescence of top leaves (Sadras *et al.*, 1993).

The linear phase of dry matter accumulation in grain starts approximately 1 week after anthesis in sunflower (Connor and Hall, 1997) and 2 weeks after silking in maize (Cirilo and Andrade, 1994). Two weeks after flowering, i.e. at an early stage of grain growth, lack of grain delayed senescence in sunflower and accelerated senescence in maize, as indicated by changes in leaf chlorophyll (Fig. 3). Leaf nitrogen was a less sensitive response variable (Fig. 4). Functionally, however, both species had a similar, and comparatively late response to treatment as feedback inhibition of photosynthesis was first detected 30–35 d after flowering (Fig. 5).

Both hormonal and nutritional signals have been invoked to account for the effect of sinks on leaf senescence. Importantly, the lack of interaction between treatment and leaf position for the first response to reproductive growth—2 weeks after flowering—indicates that the signal, whatever its nature, was equally effective throughout the plant in both species. Thomas (1992) proposed that leaf senescence could be triggered by shortage or excess assimilate, thus defining a 'window' between an upper and a lower threshold; as long as a leaf is within this window, senescence is not initiated. Accordingly, lack of grain in sunflower could have delayed senescence because leaves were able to maintain assimilate content above the lower threshold. In maize, accelerated senescence associated with lack of grain might have been related to the build up of assimilate above the upper threshold. Feedback inhibition of photosynthesis

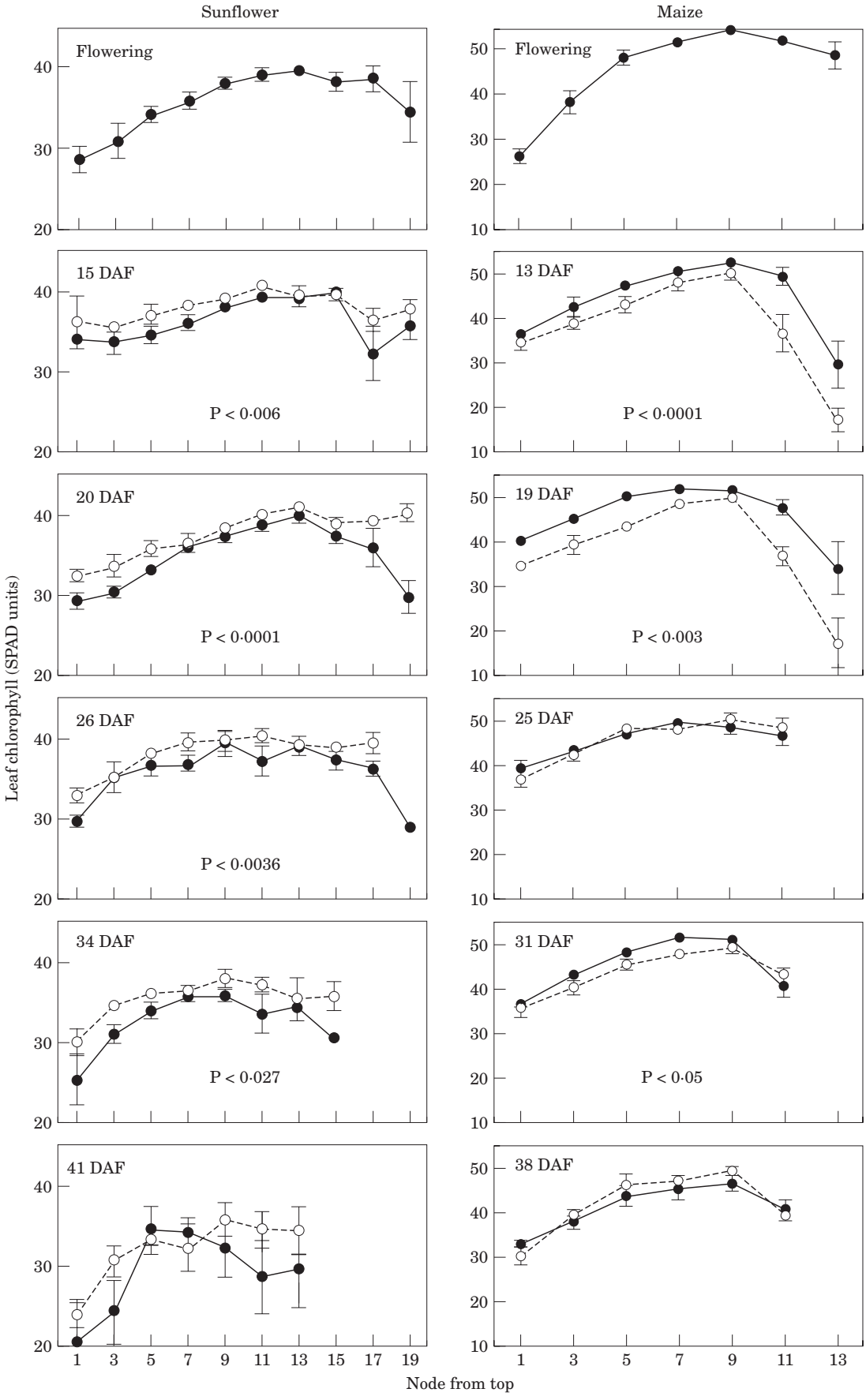

FIG. 3. Effect of reproductive growth on the profiles of leaf chlorophyll in sunflower and maize. *P* values indicate treatment effects. ○, −G; ●, +G. Bars are 2 s.e.m.

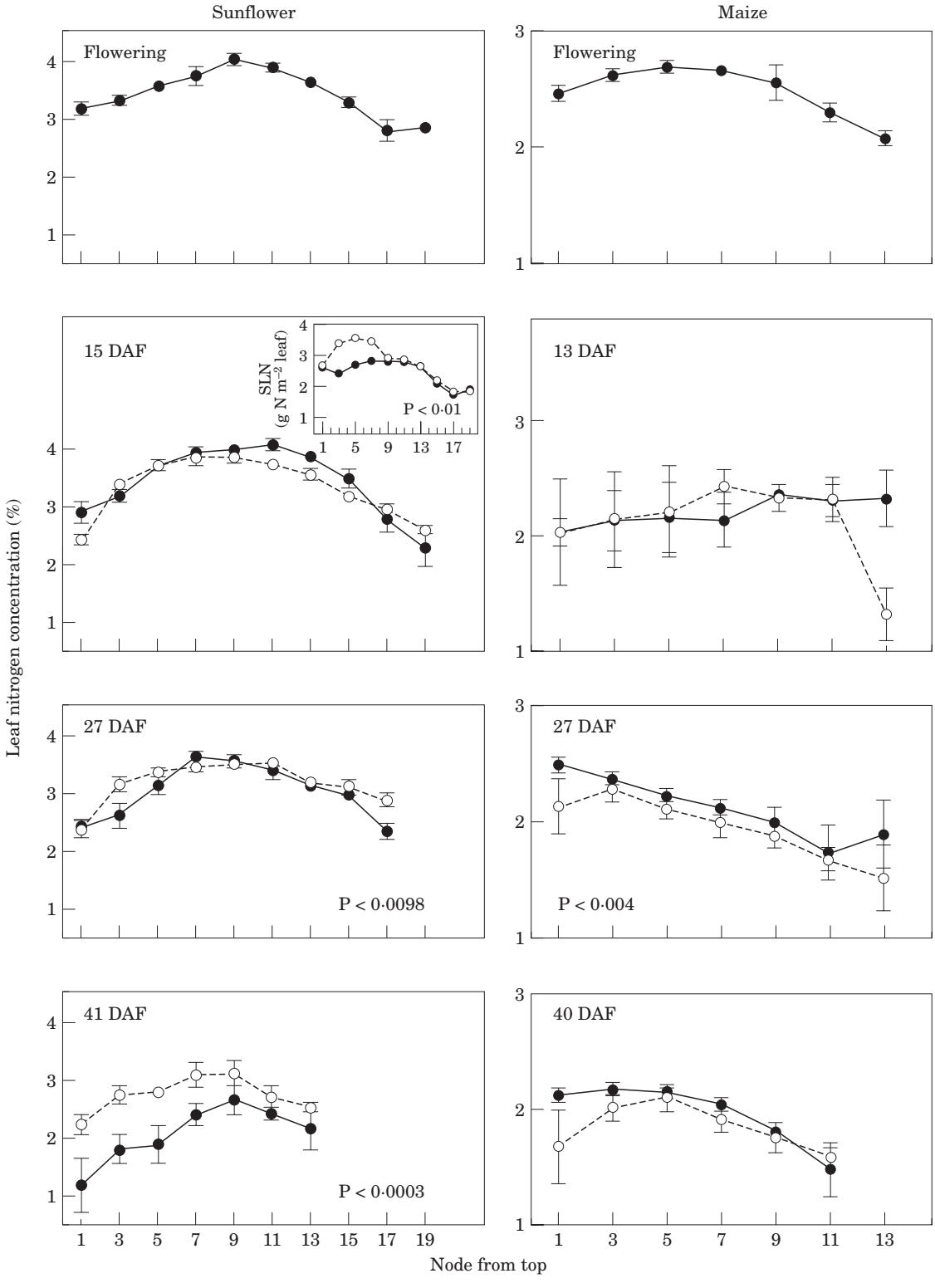

FIG. 4. Effect of reproductive growth on the profiles of leaf nitrogen in sunflower and maize. Inset shows nitrogen content on a leaf-area basis (SLN). *P* values indicate treatment effects. ○, −G; ●, +G. Bars are 2 s.e.m.

(Evans, 1993) was first detected, however, at 30–35 DAF (Fig. 5), in comparison to the first evidence of treatment effect on senescence detected at 13–14 DAF (Figs 2 and 3). Hence, unless the upper threshold for senescence in maize is much lower than the build up of assimilate required to reduce photosynthesis, it is unlikely that the accelerated

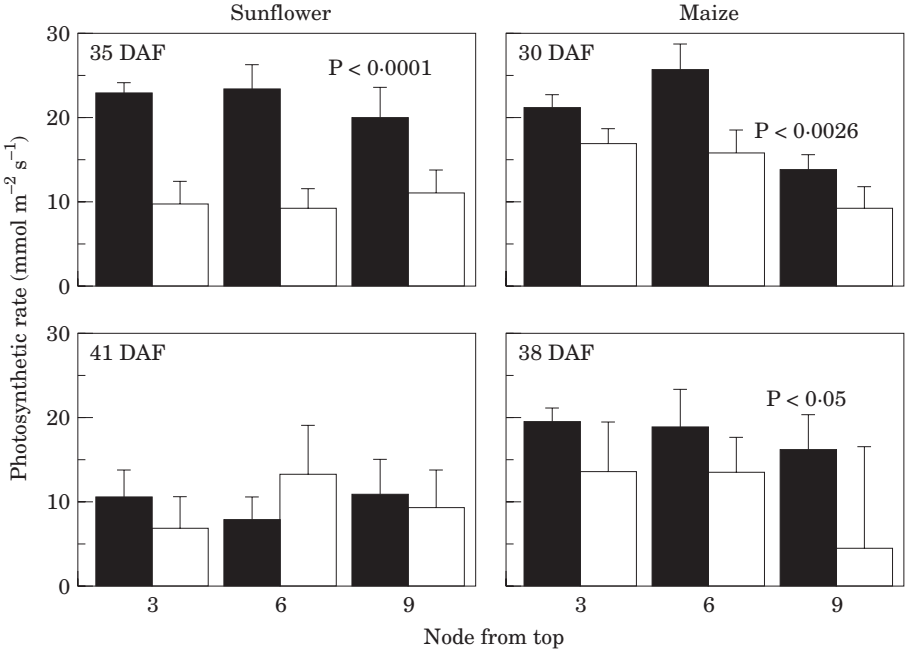

FIG. 5. Effect of reproductive growth on the photosynthetic rate in leaves of sunflower and maize. *P* values indicate treatment effects. ■ +G; □ −G. Bars are 1 s.e.m.

senescence of −G maize leaves was mediated by excess assimilate. Furthermore, stems of −G maize can act—for up to 3 weeks after flowering—as an alternative sink able to accumulate carbohydrate that would otherwise have gone to grain (Dalla Valle, 1998). In addition to carbon, nitrogen and phosphorus are important nutritional factors that could account for the delayed senescence of decapitated sunflower (Thomas, 1992). Post-anthesis nitrogen uptake from the soil is increased for 'stay-green' maize (Tollenar and Dwyer, 1999) but no mechanism has been advanced involving mineral nutrients that could account for accelerated senescence in barren maize.

Hormones including cytokinins could, in principle, account for delayed but not for accelerated senescence in response to lack of grain. It is well established that cytokinins may delay leaf senescence (Richmond and Lang, 1957). Thus, maintenance of root activity in −G plants, and the consequent maintenance of cytokinin synthesis and its transport to the shoot, could be involved in sunflower but not in maize-type responses as found in our study. Although its role on senescence is less clear (Staswick, 1992), jasmonic acid and related compounds deserve closer attention because of their contrasting effects on different plant species. In fact, methyl jasmonate seems to fit well in the sunflower-maize system under study as it is more effective in accelerating chlorophyll loss in grasses than in dicots; moreover, it showed a delaying effect in some dicots, including *Phaseolus coccineus* (Hall and Horton, 1994).

ACKNOWLEDGEMENTS

We thank Dr M. Cecilia Rousseaux for comments on the manuscript and Fundación Antorchas for financial support (Grant A-13388/1-2). VOS and FHA are members of, and LE holds a scholarship from, CONICET – the Research Council of Argentina.

LITERATURE CITED

Andrade FH. 1995. Analysis of growth and yield of maize, sunflower and soybean grown at Balcarce, Argentina. *Field Crops Research* **41**: 1–12.

Cirilo AG, Andrade FH. 1994. Sowing date and kernel weight in maize. *Crop Science* **36**: 325–331.

Connor DJ, Hall AJ. 1997. Sunflower physiology. In: Schneiter AA, ed. *Sunflower technology and production, monograph No. 35*. Madison: ASA, CSSA, SSSA, 113–182.

Crafts-Brandner SJ, Poneleit CG. 1987. Effect of ear removal on CO_2 exchange and activities of ribulose bisphosphate carboxylase/oxygenase and phosphoenolpyruvate carboxylase of maize hybrids and inbred lines. *Plant Physiology* **84**: 261–265.

Dalla Valle DE. 1998. *Dry matter production and silage quality in forage maize with different kernel number*. MSc Thesis, University of Mar del Plata, Argentina.

Drouet J-L, Bonhomme R. 1999. Do variations in local leaf irradiance explain changes to leaf nitrogen within row maize canopies? *Annals of Botany* **84**: 61–69.

Evans LT. 1993. *Crop evolution, adaptation and yield*. Cambridge: Cambridge University Press.

Hall SJ, Horton RF. 1994. Methyl jasmonate and bean leaf abscission. *Plant Growth Regulation* **14**: 187–192.

Hall AJ, Chimenti CA, Vilella F, Freier G. 1985. Timing of water stress effects on yield components in sunflower. *Proceedings 11th Sunflower Conference, 10–13 March 1985, Mar del Plata,* 131–136.

Ho I, Below FE. 1989. Whole plant senescence of sunflower following seedhead removal. *Plant Physiology* **91**: 85–90.

Ho I, Below FE, Hageman RH. 1987. Effect of head removal on leaf senescence of sunflower. *Plant Physiology* **83**: 844–848.

Inskeep WP, Bloom PR. 1985. Extinction coefficients of chlorophyll *a* and *b* in N,N-dimethylformamide and 80% acetone. *Plant Physiology* **77**: 483–485.

Lindoo SJ, Noodén LD. 1977. Studies on the behaviour of the senescence signal in Anoka soybeans. *Plant Physiology* **59**: 1136–1140.

Lu Z, Neumann PM. 1998. Water-stressed maize, barley and rice seedlings show species diversity in mechanisms of leaf growth inhibition. *Journal of Experimental Botany* **49**: 1945–1952.

Merrien A, Grandin L. 1990. Comportement hydrique du tournesol. Synthèse des essais 'Irrigation 1983–1988'. In: Blanchet R, Merrien A, eds. *Le tournesol et l'eáu. Adaptation à la sécheresse. Réponse à l'irrigation*. Paris: CETIOM, 75–90.

Miceli F, Crafts-Brandner SJ, Egli DB. 1995. Physical restriction of pod growth alters development of soybean plants. *Crop Science* **35**: 1080–1085.

Nelson DW, Sommers LE. 1973. Determination of total nitrogen in plant material. *Agronomy Journal* **65**: 109–112.

Richmond A, Lang A. 1957. Effect of kinetin on protein content and survival of detached *Xanthium* leaves. *Science* **13**: 650–651.

Rousseaux MC. 1997. *Control lumínico de la senescencia foliar pre-antesis en el cultivo de girasol*. PhD Thesis, University of Buenos Aires, Argentina.

Rousseaux MC, Hall AJ, Sánchez RA. 1993. Far-red enrichment and photosynthetically active radiation level influence leaf senescence in field-grown sunflower. *Physiologia Plantarum* **96**: 217–224.

Sadras VO, Hall AJ, Connor DJ. 1993. Light-associated nitrogen distribution profile in flowering canopies of sunflower (*Helianthus annuus* L.) altered during grain filling. *Oecologia* **95**: 488–494.

Staswick PE. 1992. Jasmonate, genes, and fragrant signals. *Plant Physiology* **99**: 804–807.

Thomas H. 1992. Canopy survival. In: Baker NR, Thomas H, eds. *Crop photosynthesis: spatial and temporal determinants*. Amsterdam: Elsevier Science, 11–41.

Thomas H, Smart CM. 1993. Crops that stay green. *Annals of Applied Biology* **123**: 193–219.

Tollenar M, Dwyer LM. 1999. Physiology of maize. In: Smith DL, Hammel C, eds. *Crop yield. Physiology and processes*. Berlin, Heidelberg: Springer-Verlag, 169–204.

Wolfe DW, Henderson DW, Hsiao TC, Alvino A. 1988*a*. Interactive water and nitrogen effects on senescence of maize. I. Leaf area duration, nitrogen distribution, and yield. *Agronomy Journal* **80**: 859–864.

Wolfe DW, Henderson DW, Hsiao TC, Alvino A. 1988*b*. Interactive water and nitrogen effects on senescence of maize. II. Photosynthetic decline and longevity of individual leaves. *Agronomy Journal* **80**: 865–870.