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Bioclimatology

Source–sink relationships in maize grown in a cool-temperate area

SA Uhart, FH Andrade

EEA Balcarce, Instituto Nacional de Tecnologia Agropecuaria (INTA), Facultad de Ciencias Agrarias, Univ Nac de Mar del Plata, CC 276 (7620) Balcarce, Buenos Aires, Argentina

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Summary — The objectives of this work were to: a), establish whether maize yield in Balcarce (Argentina 37°45'LS; 58°18'LO) is limited by the source of assimilates or by the number and size of the reproductive sinks; b), establish whether hybrids that differ in length of the growing cycle present differences in their source–sink relationships; c), determine to what extent the evolution of carbohydrate (CH) reserves in the plant is modified by different source–sink relationships. The experiment was conducted at Balcarce over a 2-year period with 2 hybrids (short season: SPS 240, long season: D2F11). The treatments consisted of 2 levels of source reduction (45 and 55% shading during the grain filling period, GFS), 2 levels of reproductive sink reduction (45 and 55% shading aroung flowering, FS) and an unshaded control. The different shading treatments had a constant reduction of radiation with variable shading duration (30–38 days). The results indicate the existence of a colimitation by source of assimilates and reproductive sinks because grain yield dropped similarly in response to shading during the flowering and the grain filling periods. FS reduced grain number/unit area and slightly increased 1 000 kernel weight. GFS reduced 1 000 kernel weight, and to a lesser extent grain number/unit area. The study of dry matter and CH accumulation or remobilization in response to shading at the R3–R5 period, relative to those of the control treatment, was useful to indicate trends toward sink or source limitations. Relative to the control, shading at any period produced a decrease in stem CH content during the treatment period. During the post-shading period, the FS treatments presented a greater CH accumulation in stems than the control. This is explained by the decrease in reproductive sink number that produced a drop in their demand of CH and by the increased importance of the stem as an alternative sink for assimilates. GFS treatments produced a strong increase in CH remobilization rate from stem during the treatment period. The 2 hybrids did not show statistically significant differences in their source–sink relationship. Nevertheless, a tendency toward a source limitation was evident in the long season hybrid.

***Zea mays* = maize / source–sink relationships / carbohydrate remobilization**

Résumé — Rapports source-puits du maïs dans une région tempérée-froide. *Les objectifs du travail ont été :*
– d'établir si le rendement en grain du maïs à Balcarce (Argentine –37°45' LS; 58°18' LO) est limité par la source d'assimilats ou par le nombre et la taille des puits reproductifs;
– d'établir si les hybrides de différents cycles ont différents rapports source-puits;
– de déterminer dans quelle mesure l'évolution des carbohydrates de réserve (CH) dans la plante est modifiée par les différentes relations source-puits. L'expérience a été conduite à Balcarce pendant 2 années avec 2 hybrides (cycle court : SPS 240; cycle long : D2F11).
Les traitements ont compris 2 niveaux de réduction de source (45 et 55% d'ombrage artificiel pendant la période de remplissage du grain, GFS), 2 niveaux de réduction des puits reproductifs (45 et 55% d'ombrage artificiel en floraison, FS), et un témoin sans ombrage artificiel.
Les différents traitements d'ombrage ont eu une réduction constante de rayonnement et une durée de la période d'ombrage variable (30–38 j).
Les résultats indiquent l'existence d'une limitation à la fois par la source d'assimilats et par les puits reproductifs parce que le rendement en grain a diminué de façon similaire en réponse aux traitements d'ombrage pendant la floraison et le remplissage du grain (tableau VI).
FS réduit le nombre de grains/unité de surface et en conséquence, on constate une légère augmentation du poids de 1 000 grains. GFS réduit le poids de 1 000 grains, et en moindre mesure, le nombre de grains/unité de surface (tableau III).
Le suivi de l'accumulation et de la remobilisation de matière sèche et des CH en réponse à l'ombrage pendant la période R3–R5 par rapport à celles du traitement témoin, a été utile pour indiquer les tendances vers des limitations par la source ou par les puits. L'ombrage à n'importe quelle période produit une réduction de CH de la tige, par rapport au témoin, pendant le temps d'imposition des traitements. Les traitements FS ont montré pendant la période post-

ombrage une plus grande accumulation de CH dans les tiges que le témoin. Ceci est expliqué par la réduction du nombre de puits reproductifs qui produit une diminution de la demande de CH, mais aussi par l'augmentation de l'importance de la tige comme puits d'assimilats.
Les traitements GFS ont produit une forte augmentation du taux de remobilisation de CH de la tige pendant le temps d'imposition du traitement (figs 3, 5 et 6; tableau IV et V).
Les 2 hybrides n'ont pas montré des différences significatives dans leurs relations source-puits. Cependant l'hybride de cycle long a montré une tendance plus évidente vers la limitation par la source, par une importance plus grande des remobilisations.

Zea mays = *maïs / relations source-puits / remobilisation de carbohydrates*

INTRODUCTION

Limitations of grain yield in crops that are not explained by unfavorable factors such as diseases, nutrient or water deficiencies, etc, may be analyzed in terms of assimilate supply to the developing grain, the source, and the potential of the grains to accomodate assimilates, the sink (Tollenaar, 1977). Among grain crops, the source–sink relationships have been studied more extensively in wheat and barley (Tollenaar, 1977). Some authors have reported that grain yield was limited by the sink capacity (Bingham, 1967; Evans and Rawson, 1970); others have concluded that yield was limited by the source (Welbank *et al,* 1966; Simpson, 1968), whereas Fischer (1975) and Stoy (1976) have suggested that both sink and source limitations may occur, and the particular combination of genotype and environment determines which limitation predominates.

Yoshida (1972), in a review, concluded that under favorable climate and adequate nutrient provision it is more likely that the sink limits grain yield of wheat and rye.

Studies on maize conducted in Mexico have shown the importance of the sink limitation on the grain yield (Yamaguchi, 1974; Goldsworthy *et al,* 1974; Goldsworthy and Coleogrove, 1974).

Similar results have been found in the USA using different research methodologies such as artificial shading (Early *et al,* 1966, 1967; Prine, 1971), artificial increment of radiation during flowering or grain filling (Schoper *et al,* 1982), total or partial defoliation and ear removal (Hanway, 1969; Barnett and Pearce, 1983; Jones and Simmons, 1983), and reduction of population density at different stages of plant development (Prine, 1971). In Rhodesia (now Zimbabwe), Allison and Watson (1966) and Allison *et al* (1975) reported that a large amount of stem dry matter which could be translocated to the grain remains without remobilisation, indicating a sink limitation.

In contrast, Daynard *et al* (1969) and Hume and Campbell (1972), in Canada, showed that non-defoliated plants had an important carbohydrate (CH) translocation from stems and husks to the grain during the last moments of grain filling period suggesting a source limitation for grain yield.

Tollenaar and Daynard (1978), in Ontario, varied incident radiation by light enrichment or artificial shading aroung flowering and grain filling. They observed that grain yield was more affected by the alteration of assimilate supply during grain filling than around flowering, and concluded that the source was the prevailing limitation.

In areas such as Ontario where the growing season of maize is restricted by cool temperatures in spring and fall, the source limitation is caused by the precocity of flowering that produces plants with small leaf area, and by the high rate of dry matter accumulation in the grains (trait chosen for areas with short grain filling period) that may cause early leaf senescence (Tollenaar and Daynard, 1982).

Early *et al* (1967), Hanway (1969), Hicks *et al* (1977), Barnett and Pearce (1983) and Vasilas and Seif (1985) reported differential hybrid responses to treatments of source or sink limitation. Most of these differences were attributed to duration of life cycle (long *vs* short).

The objectives of this study were: a) to determine if maize grain yield in Balcarce, Argentina, is limited by the capacity of the reproductive sinks; b) to evaluate the effect of the length of the growing cycle in the source–sink relationships; c) to determine to what extent the evolution of stem CH is affected by the different source–sink relationships.

The methodology of assimilate reduction during flowering and grain filling (Tollenaar, 1977; Tollenaar and Daynard, 1978) was used, taking into account the considerations made by Tollenaar and Daynard (1978), Lauer (1985) and Early *et al* (1966, 1967) with relation to type and intensity of the treatment.

MATERIALS AND METHODS

The experiment was conducted during the 1987/1988 and 1988/1989 growing seasons at the INTA Research Station Balcarce, Buenos Aires, Argentina (37°45' LS; 58°18' LO) on a typic Argiudol soil with a minimum effective depth of 1.50 m (25.9% clay; 40% silt; 34% sand, and 5.3% organic matter at a depth of 0–25 cm). This study involved two red, flint simple hybrids of maize: Dekalb 2F11 (long season, 3300 °C from emergence to physiological maturity; Ontario method; Brown, 1969) and SPS 240 (short season, 2800 °C from emergence to physiological maturity; Ontario method; Brown, 1969).

They were sown on 16 October 1987 and 12 October 1988, rows 0.7 m apart. The population density was 85 000 plants/ha in 1987/1988 and 91 000 plants/ha in 1988/1989.

The crop was kept free of weeds, and insect pests were adequately controlled.

The experimental site was fertilized with 102 kg/ha of P2O5 and 128 kg/ha of N in 1987/1988, and 65 kg/ha of P2O5 and 140 kg/ha of N in 1988/1989.

Soil water content was kept above 60% of the maximum available water value in the first meter of depth by irrigation (254 mm in 1987/1988 and 185 mm in 1988/1989).

The treatments were: an unshaded control, 45 and 55% shading (determined by means of a line quantum sensor) around flowering (V11–V12/R3), FS; and 45 and 55% shading during grain filling (R3/R5), GFS. (V11 = 11th leaf, R3 = milk grain, R5 = visible dent; Ritchie and Hanway, 1982).

The shading periods were of variable duration (30–38 days; table I) and constant incident radiation (average total irradiation received by the subplots above shading cloth was 721 MJ/m^2, CV : 2.2%). Plots were shaded with cloths of different mesh, 12 m long, 2.3 m wide, stretched on cane and wire structures. Differences of 1–2 °C in average air temperature between shaded and unshaded plots were recorded.

The experimental design was a split-plot with the hybrids as main plots and shading treatments as subplots. The main plots were disposed in randomized complete blocks with four replications in 1987/1988 and three replications in 1988/1989. The subplots consisted of four rows of 12 m (with one border row on each side). The evolution of total above-ground plant dry weight and its partitioning was followed.

Plant samples were taken every 20–30 days. The sample size was 6 plants in 1987/1988 and 10 plants in 1988/1989. Plants parts were oven-dried at 65 °C to constant weight, and weighed.

Leaf area was determined using a AAC-400 area meter by Hayashi Denfoh Co Ltd, Japan.

Mean crop growth rate (CGR), net assimilation rate (NAR) and leaf area duration (LAD) were calculated according to Kvet *et al* (1971) and Gardner *et al* (1985).

Percent photosynthetically active radiation (PAR) interception by the crop was calculated as (1-*I*/*Io*) x 100, where *I* is the incident PAR at ground level, and *Io* is the incident PAR at the top of the canopy. These values were obtained with a LICOR 188 B radiometer connected to a 191 SB line quantum sensor. Determinations were taken periodically (every 15 days), following the technique described by Gallo and Daughtry (1986) for sensor placement and number of observations. Measurements were confined to ± 1 h from solar noon to eliminate the effect of solar altitude on the interception values. Measurements were taken on sunny days. The PAR intercepted by the shading cloths was calculated by placing the line quantum sensor 15 cm above and below it. This measurements were taken from 9 am to 4 pm.

Stem CH was determined following the method described by Weinmann (Weinmann, 1947; Berger, 1984). Samplings were taken at the V11–V12, R3; R5 and R6 phenological stages (Ritchie and Hanway, 1982). Each sample consisted of 5 plants (only the ear and the ear-1 internodes were considered; Daynard *et al*, 1969; Barnett and Pearce, 1983; Jones and Simmons, 1983). These internodes were oven-dried at 60 °C to constant weight and ground (1-mm mesh screen). Total stem CH (kg/ha) was calculated as the product of CH concentration (on dry weight basis) and stem dry weight (Welton *et al*, 1930; Daynard *et al*, 1969).

Table I. Phenological stages.

Year	*Hybrid*	*Sowing date*	*Emergence date*	*V11/V12*	*50% silking*	*R3*	*R5*	*R6*
87/88	SPS 240	16/10	28/10	19/12(52)	3/1(67)	19/1(83)	25/2(120)	9/3(132)
	D2F11	16/10	28/10	30/12(63)	18/1(82)	30/1(93)	10/3(134)	4/4(160)
88/89	SPS 240	12/10	26/10	20/12(55)	2/1(68)	18/1(84)	22/2(119)	7/3(132)
	D2F11	12/10	26/10	29/12(64)	16/1(82)	27/1(93)	7/3(132)	29/3(154)

( ) : days after emergence

Stem CH remobilization to the ear and stem accumulation were calculated as the difference between total stem CH in R3 and R5. After R5 dry matter losses (tassel parts and the stem top) confound the calculation.

Total CH remobilization rate was estimated as the ratio between total CH remobilization and days between R3–R5.

Total CH remobilization efficiency was calculated as the ratio between total CH remobilization and stem CH content in R3. Similar criteria were followed to calculate vegetative dry matter remobilization.

Potential kernel number/ear was visually recounted on 3 ears/subplot at flowering by means of a magnifying glass. Two rows of 7.15 m length were harvested, and grain moisture recorded. Grain yield (14% moisture) and grain yield components were determined.

Harvest index (HI) was calculated as the quotient between grain yield (on dry basis) and total above-ground dry matter.

RESULTS AND DISCUSSION

Table II shows temperature and radiation data for the different phenologic periods, and table I shows the phenological stages for both years.

Total incident solar radiation was similar both years. Mean daily temperatures were higher in the second than in the first season at all the phenological stages.

Crop growth and development

Total above-ground dry matter accumulation was, up to R5, a function of the incident radiation (fig 1). Dry matter losses occurred between R5–R6 (senescent leaves, panicles, etc). The lowest values of total dry matter accumulation corresponded to treatment GFS 55%. This is explained by the lowest ear dry matter accumulation in this treatment.

Shading around flowering reduced assimilate partitioning to the ear during the reproductive growth in relation to the control treatment (fig 2), and largely increased reserves in stem + sheaths (fig 3), and to a lower extent in leaves (fig 4) during the grain filling period.

From R_3 to R_5, crop growth rates of the FS treatments were similar to those of the control.

Shading around flowering produced a reduction in the number of grains/unit area (table III). The stem became an important sink, accumulating large amounts of carbohydrates (figs 3 and 5). Conversely, shading during the grain filling period induced a great remobilization of reserves from stems generated by the unbalanced relationship between the demand for assimilates by the reproductive sinks and the crop photosynthetic rate. Similar trends were reported by Tollenaar and Daynard (1982), Barnett and Pearce (1983), and Reed *et al* (1988).

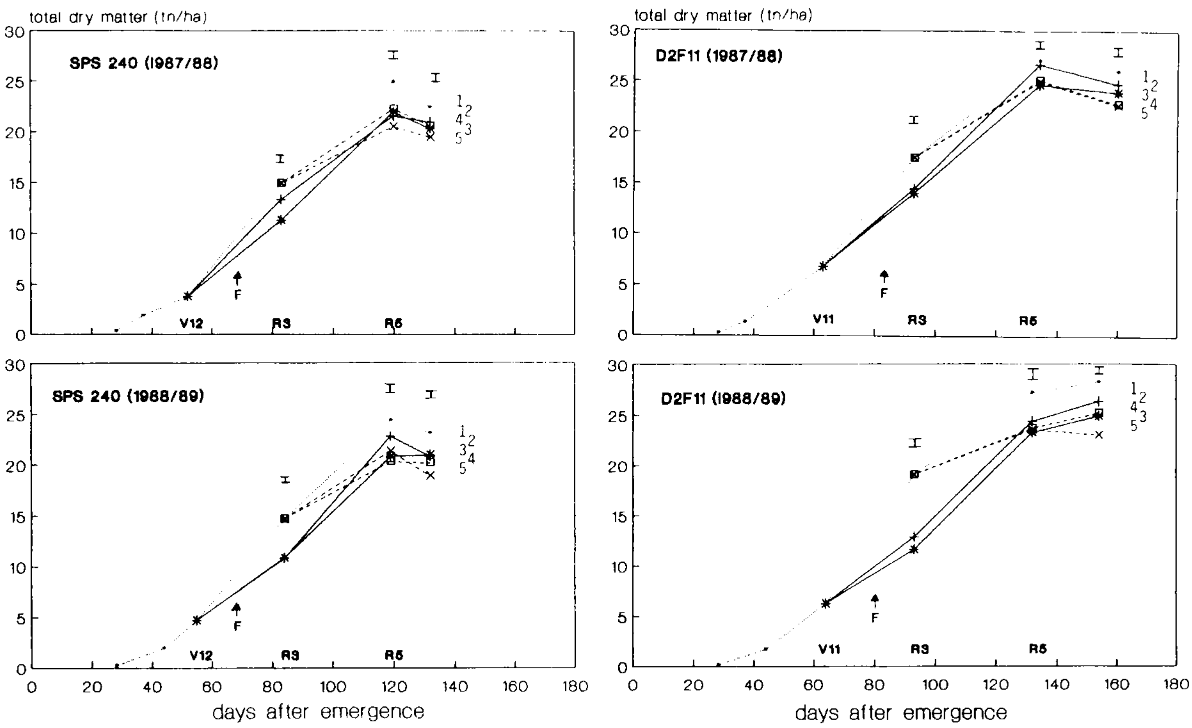

Fig 1. Evolution of above-ground total dry matter for two hybrids, five shading treatments and two growing seasons. Bars indicate the standard error of the shading treatment means. Shading treatments: 1 = control (◫); 2 = 45% FS (+); 3 = 55% FS (•); 4 = 45% GFS (❑); 5 = 55% GFS (x).

Table II. Minimum, maximum and mean temperature, and mean global radiation received by crop at different phenological periods.

Year	*Hybrid*	*Phenological period* +																			
		1	*2*	*3*	*4*	*5*	*1*	*2*	*3*	*4*	*5*	*1*	*2*	*3*	*4*	*5*	*1*	*2*	*3*	*4*	*5*
		T min (°C)					*T max (°C)*					*T mean (°C)*					*Incident solar radiation (MJ m–2)*				
87/88	SPS 240	8.9	9.7	12.1	12.0	12.5	21.2	24.7	26.5	24.4	25.1	15.0	17.2	19.3	18.2	18.8	559.17	606.59	747.32	721.97	209.62
	D2F11	8.9	9.5	12.4	12.4	11.5	21.2	24.5	28.0	24.2	22.5	15.0	17.0	20.2	18.3	17.0	559.17	824.22	721.95	707.45	332.45
88/89	SPS 240	7.5	13.4	13.3	13.3	13.0	23.3	24.0	28.3	28.1	26.8	15.4	18.7	20.8	20.7	19.9	505.99	596.38	721.10	718.13	229.23
	D2F11	7.5	13.0	13.8	13.4	11.3	23.3	24.8	29.2	27.2	24.7	15.4	18.9	21.5	20.3	18.0	505.99	818.72	693.81	735.50	322.80

+ 1: Emergence/V4-V5; 2: V4-V5/V11-V12; 3: V11-V12/R3 (shading around flowering); 4: R3/R5 (shading during grain filling); 5: R5/R6 (Ritchie and Hanway, 1982).

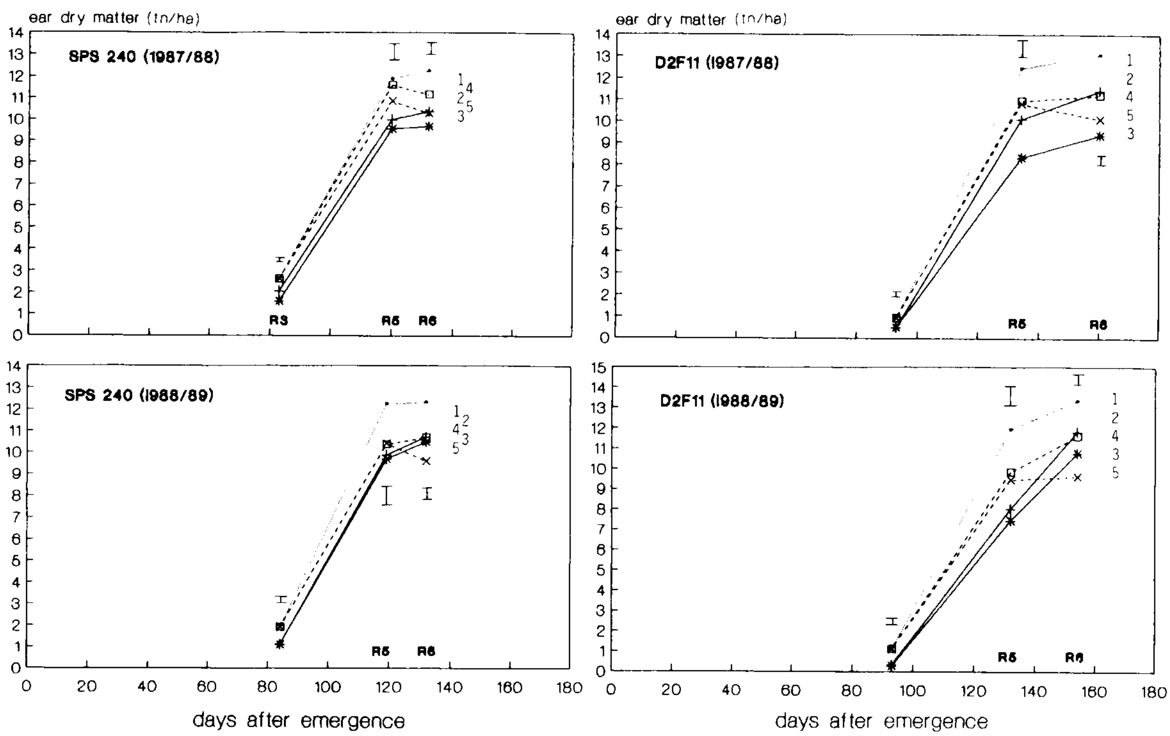

Fig 2. Evolution of ear dry matter for 2 hybrids, 5 shading treatments and 2 growing seasons. Bars indicate the standard error of the shading treatment means. Shading treatments : 1 = control (□); 2 = 45% FS (+); 3 = 55% FS (•); 4 = 45% GFS (□); 5 = 55% GFS (x).

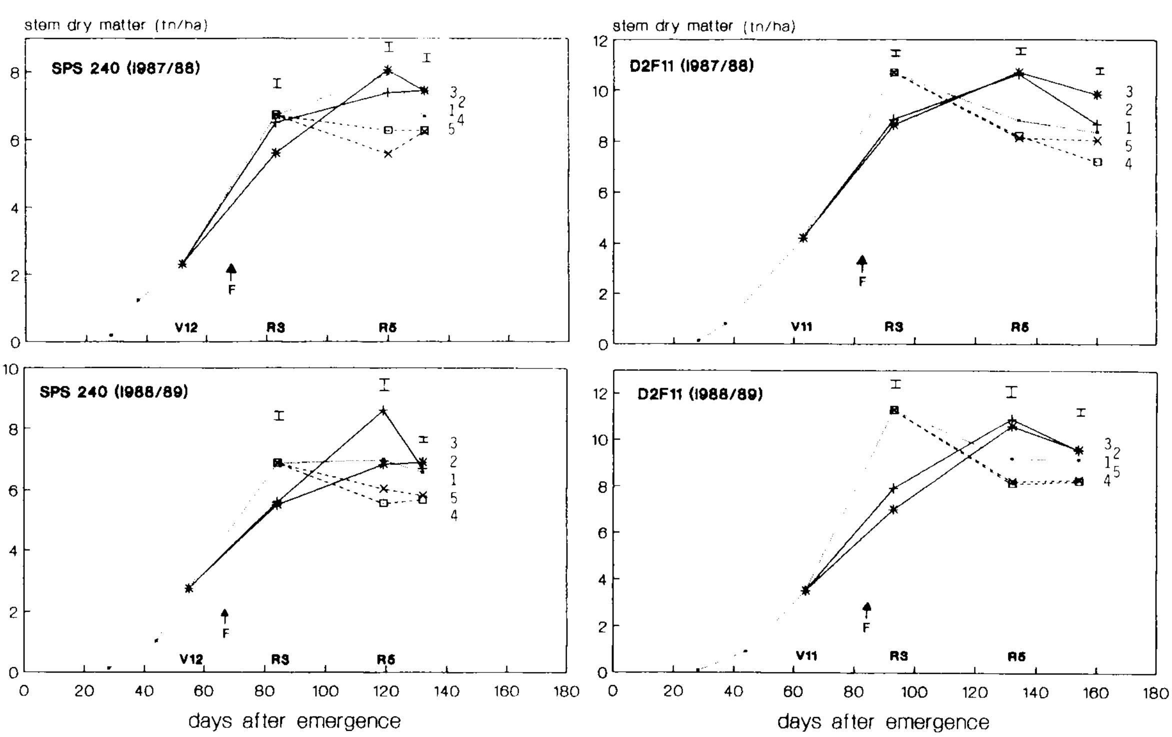

Fig 3. Evolution of stem + sheath dry matter for 2 hybrids, 5 shading treatments and 2 growing seasons. Bars indicate the standard error of the shading treatment means. Shading treatments: 1 = control (□); 2 = 45% FS (+); 3 = 55% FS (*); 4 = 45% GFS (□); 5 = 55% GFS (x).

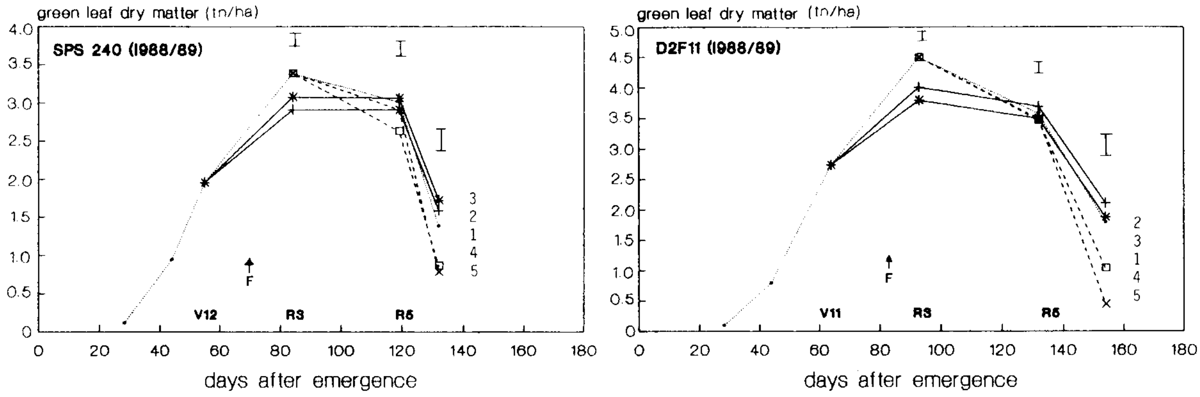

Fig 4. Evolution of green leaf dry matter for 2 hybrids and 5 shading treatments in 1988/1989 growing season (the growing cycle 1987/1988 was similar to second year). Bars indicate the standard error of the shading treatment means. Shading treatments : 1 = control (□); 2 = 45% FS (+); 3 = 55% FS (⋆); 4 = 45% GFS (❑); 5 = 55% GFS (x).

During the R3–R5 period the stem dry matter of the control treatment showed an increase for hybrid SPS 240 and a drastic reduction for hybrid D2F11. This provides evidence of the predominance of source or sink limitation.

Dry matter accumulation in green leaves (fig 4; only one-year data are shown since both seasons presented similar results for this variable) presented similar trends to those found for the evolution of stem + sheaths dry matter. Leaf dry matter diminished during the flowering shading with respect to the control, but it surpassed the latter after that shading period. Two reasons would explain this phenomenon: a) since shading at flowering generated a lower number of reproductive sinks, part of the photosynthates went to alternative sinks; however, the leaves are not an important CH reservoir in maize; b) the lower number of grains reduced the CH and N remobilization, producing a greater leaf area

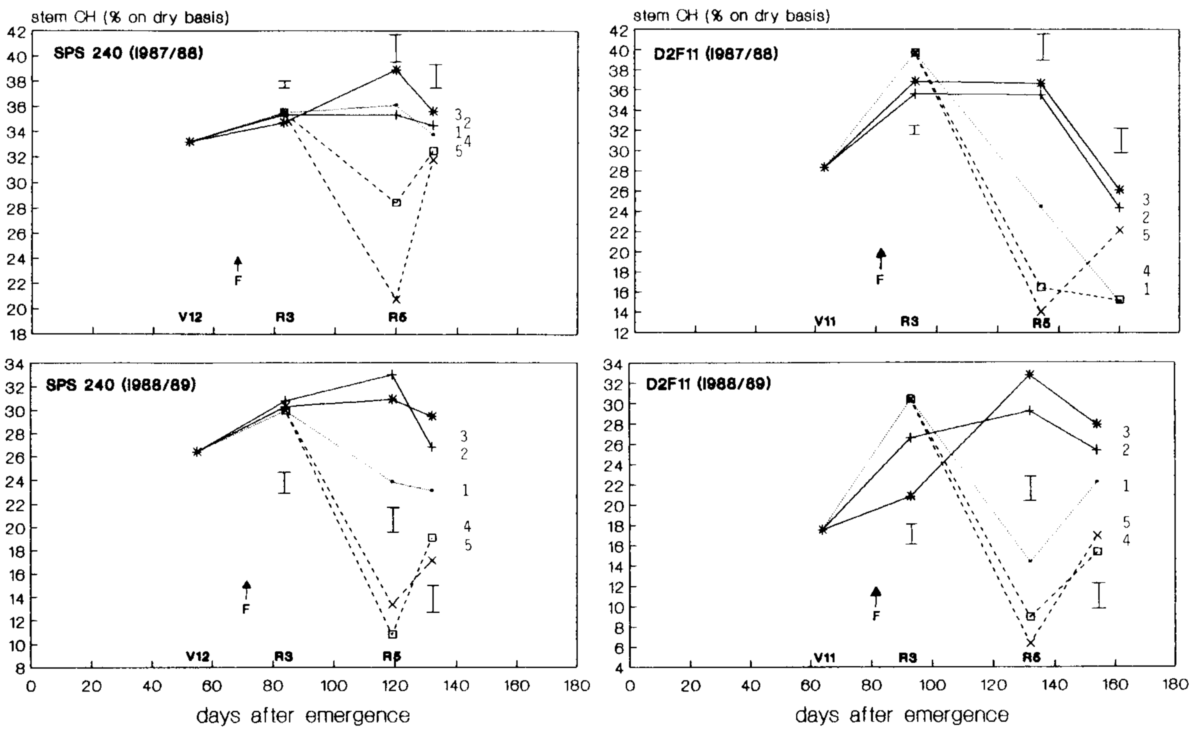

Fig 5. Evolution of stem non-structural carbohydrates of 2 hybrids, 5 shading treatments and 2 growing seasons. Bars indicate the standard error of the shading treatment means. Shading treatments : 1 = control(□); 2 = 45% FS (+); 3 = 55% FS (⋆); 4 = 45% GFS (❑); 5 = 55% GFS (x).

Table III. Grain yield and yield components (percent values relative to control of each hybrid).

Yield components	*Treatment number* + 1	2	3	4	5	*SE*	*a*++	*b*++	*c*++
87/88 SPS240									
Kernel number	100	84.8	78.3	98.0	93.5	2.40	x	xx	NS
Kernel weight	100	99.3	100.8	93.5	90.0	1.58	x	xx	x
Grain yield	100	83.9	78.6	91.4	84.3	1.93	NS	xx	x
88/89 SPS 240									
Kernel number	100	84.7	82.3	96.3	90.0	2.52	NS	xx	NS
Kernel weight	100	103.0	103.0	90.7	87.0	2.36	NS	xx	NS
Grain yield	100	86.6	84.9	87.3	78.4	2.21	NS	xx	NS
87/88 D2F11									
Kernel number	100	78.5	64.3	86.5	82.0	2.40	x	xx	NS
Kernel weight	100	110.5	110.0	99.5	95.5	1.58	x	xx	x
Grain yield	100	86.7	70.6	85.4	77.9	1.93	NS	xx	x
88/89 D2F11									
Kernel number	100	85.0	74.3	96.0	82.0	2.52	NS	xx	NS
Kernel weight	100	103.7	106.0	90.3	80.3	2.36	NS	xx	NS
Grain yield	100	87.7	78.8	86.5	72.5	2.21	NS	xx	NS

+ Treatments: 1 = Control; 2 = FS45%; 3 = FS55%; 4 = GFS45%; 5 = GFS55%. ++ a, b, c : significance of differences between hybrids, shading treatments and hybrid x shading treatment interaction (analysis of percentage data was made according to Steel and Torrie, 1960). x, xx, NS : 5%, 1% significance and no significance respectively.

duration (LAD). This concept is based on the self-destruction theory proposed by Sinclair and de Wit (1976) in soybeans, and on the concepts formulated by Leopold (1961), Moss (1962) and Tollenaar (1986). Significant differences (5%) in LAD were detected among the treatments during the R5–R6 period for the second growing season. For both hybrids, the values were highest for FS, lowest for GFS and intermediate for the control. The acceleration of senescence under a high source-sink relationship (Christensen *et al,* 1981) is observed as a response to drastic reductions in reproductive sink capacity (for example total ear elimination) that are far from the sink reduction achieved in this experience.

On the other hand, the greater relative demand of the growing kernels in the GFS treatments produced a higher assimilate partition to the grain and a higher CH and N remobilization from the leaves during the grain filling period. Similar results were presented by Tollenaar and Daynard (1982) and Reed *et al* (1988). The FS treatments diminished ear dry matter accumulation (fig 2) and the number of reproductive sinks. Upon removal of the shading cloths at R3, ear growth rate was lower than that of the control and in some cases even lower than that corresponding to GFS.

Since crop growth rates between R3–R5 were similar for the control and FS treatments, it is inferred that the lower number of grains/unit area did not affect the photosynthetic rate but it did modify the assimilate partitioning. The stems, sheaths and husks accumulated more dry matter when the crop was shaded around flowering, while the opposite occurred with the ears. Consequently no evidence of feed-back regulation of photosynthesis by a reduced reproductive sink demand was found.

The GFS treatments reduced ear dry matter accumulation through a reduction in photosynthetic rate. These treatments presented the lowest total dry matter accumulation during the R3–R5 period. Upon removal of the shading cloths, the GFS treatments (R5–R6) also presented lower ear growth rate than the rest of the treatments. Similar results were reported by Tollenaar and Daynard (1978) and Reed *et al* (1988).

This could be explained by the fact that the effective grain filling period was shortened as a response to a low amount of reserves to meet the reproductive sink demand (Daynard and Duncan, 1969; Daynard *et al,* 1971). The lowest values in green leaves dry matter and LAD observed for these treatments during R5–R6 period of the second year support this concept.

The FS treatments could have prolonged the effective grain filling period because of the large amount of reserves they had. The crop, stem + sheaths, leaf and ear growth rates, and also the net assimilation rate and vegetative dry matter remobilization (fig 6) showed similar behaviors to that mentioned for total dry matter.

No differences were found among shading treatments in LAI (average range at R3: 4.5–4.8 and 5.9–6.1 for SPS 240 and D2F11, respectively, and average range at R5: 3.8–4.1 and 4.2–4.7 for SPS 240 and D2F11, respectively), specific leaf weight and PAR interception. The hybrid D2F11 reached 95% PAR interception 15 days before flowering while the other hybrid (SPS 240) reached this value around flowering.

The stem CH values were modified by the shading treatments (fig 5) at all the samplings (except at R3 in the 87/88 growing season). The FS treatments reduced the stem CH less than the GFS treatments. During the respective shading periods, the GFS treatments produced a greater stem CH reduction than the FS treatments. After removing the shades the FS treatments accumulated CH in the subsequent period to shading (R3–R5). Later, during R5–R6, these CH were partially remobilized to the ear (photosynthetic rate, air temperature and solar radiation declined, leaf senescence increased, while the grain filling period still continued).

In the GFS treatments the stem CH were remobilized during the shading period (R3–R5). Upon removal of the shading cloths (R5–R6) they accumulated again in the stems, because of the early ending of the effective grain filling period and the persistence of the assimilate demand by the stem. The evolution of ear and stem dry matter supports this concept.

The reduction in the source of assimilates decreased the grain filling duration, while the reduction in reproductive sink capacity diminished the ear growth rate. The maintenance of the photosynthetic activity in the GFS treatments (with stem CH accumulation) after the end of the grain filling period, indicates that the finishing signal of grain filling would be produced within the reproductive sinks.

The stem CH level of the control treatment of hybrid SPS 240 was nearer the maximum possible accumulation than that of hybrid D2F11, while the stem CH level of the control of D2F11 was nearer the maximum remobilization (GFS) than that of hybrid SPS 240. The same trends were observed for the CH remobilization rate and efficiency (tables IV and V). For example, for SPS 240, 1987/1988 growing season, differences between CH remobilization rate of control treatment and the maximum possible accumulation and remobilization were 39 and 75 kg ha–1 day–1 respectively (table IV). The control value is nearer the maximum accumulation than the maximum remobilization. There was, therefore, a trend toward a sink limitation.

This information provides more evidence to establish the predominance of source or sink limitation.

Grain yield and yield components

The effects of plot and subplot treatments are shown in table III. The FS treatment reduced

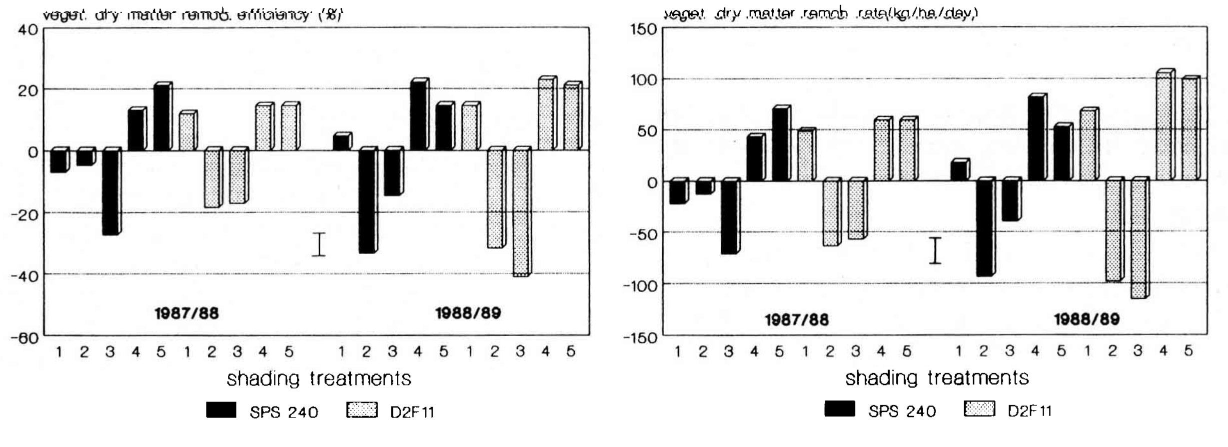

Fig 6. Vegetative dry matter (VDM) remobilization rate ([VDM R3–VDM R5]/ days between R3, R5) and vegetative dry matter remobilization efficiency ([VDM R3–VDM R5]/VDM R3), between R3–R5, for 2 hybrids, 5 shading treatments and 2 growing seasons. Bars indicate the standard error of the shading treatment means. Shading treatments : 1 = control; 2 = 45% FS; 3 = 55% FS; 4 = 45% GFS; 5 = 55% GFS.

Table IV. Comparison between the maximum values (for the trial conditions) and control treatment values of total stem CH remobilization and accumulation rate (kg ha^{-1} day^{-1}) during R3–R5 period.

Year	*SPS 240*				*D2F11*			
Treatment	*Accumulation*		*Remobilization*		*Accumulation*		*Remobilization*	
	87/88	*88/89*	*87/88*	*88/89*	*87/88*	*88/89*	*87/88*	*88/89*
	kg ha^{-1} day^{-1}				kg ha^{-1} day^{-1}			
Control	+24	–19	+24	–19	–49	–60	–49	–60
FS or GFS	+63	+66	–51	–71	+24	+78	–73	–85
Difference	39	85	75	52	73	138	24	25

Values (+) = accumulation (–) = remobilization. FS = flowering shading treatments (accumulation values); GFS = grain filling shading treatments (remobilization values).

Table V. Stem CH remobilization efficiency ([CH R3–CH R5]/CH R3) during R3–R5 period.

Treatment	*+SPS 240*					*D2F11*				
Year	*1*	*2*	*3*	*4*	*5*	*1*	*2*	*3*	*4*	*5*
			%					%		
87/88	–0.24	–0.19	–0.63	0.24	0.51	0.49	–0.21	–0.24	0.67	0.73
88/89	0.19	–0.66	–0.30	0.71	0.60	0.60	–0.54	–0.78	0.79	0.85
Average	–0.02	–0.43	–0.46	0.48	0.56	0.55	–0.38	–0.51	0.73	0.79

Negative values indicate CH accumulation. Standard error: 87/88 = 0.09; 88/89 = 0.16. + Treatments: 1 = Control 2 = FS45%; 3 = FS55%; 4 = GFS45%; 5 = GFS 55%.

grain number/unit area and increased kernel weight. The GFS treatment reduced grain weight and to a lesser extent grain number/unit area. In the 1987/1988 growing season the second ear abortion (extended to a middle of grain filling period) reduced to a greater extent the grain number/ha. The plant response under a source limitation was, in this case, to eliminate the second ears more than reduce the grain weight. No differences in potential number of grain/ear (at flowering) was found between the shading treatments.

The kernel weight of the control treatment of hybrid SPS 240 was closer to its potential weight (for the conditions of the trial) than that of hybrid D2F11.

No differences were detected in grain yield (Tukey test 5%) between shading at flowering and during grain filling (table VI). The combined year analysis shows a significant interaction year x shading treatment.

The harvest index (HI) was higher for the control, intermediate for the GFS treatments and lower for the FS treatments. These results agree with the accumulation and remobilization trends observed for those treatments.

The impact of shading during flowering on the reproductive sinks and that of shading during grain filling on the source of the assimilates were proportionally similar.

In Balcarce, grain yield is colimited by the source of assimilates during grain filling and by the reproductive sink capacity. According to the methodology proposed by Tollenaar (1977) and Tollenaar and Daynard (1978) the grain yield was affected in the same proportion by a reduction in the assimilate flux around flowering and during the grain filling period (table VI). The kernel weight of the SPS 240 control treatment was closer to its potential weight (for the conditions of the experiment) than that of the D2F11 hybrid. This fact is evidence that the SPS 240 hybrid

Table VI. Grain yield for the different treatments (kg/ha, 14% moisture).

	Growing season 87/88				*Growing season 88/89*		
Treat+	*SPS240*	*Treat+*	*D2F11*	*Treat+*	*SPS 240*	*Treat+*	*D2F11*
			kg ha⁻¹				
1	12.530 a	1	13.060 a	1	12.544 a	1	13.334 a
4	11.446 b	2	11.317 b	4	10.933 b	2	11.680 b
5	10.561 bc	4	11.147 bc	2	10.847 b	4	11.526 b
2	10.517 bc	5	10.158 cd	3	10.648 b	3	10.535 bc
3	9.847 c	3	9.196 d	5	9.824 b	5	9.652 c

Standard error to compare shading treatments: 87/88 = 253 kg/ha; 88/89 = 294.6 kg/ha. The same letters indicate no differences between shading treatments (Tukey test 5%). + Treatments: 1 = Control; 2 = FS45%; 3 = FS55%; 4 = GFS45%; 5 = GFS55%.

presented a stronger trend towards a sink limitation than the other hybrid.

Other variables provided evidence for the predominant limitation within the colimitation.

During the R3–R5 period, stem dry matter was constant or increased during the two growing seasons in the control treatment of SPS 240 hybrid. The assimilate production exceeded the grain capacity to accomodate them, indicating a tendency toward a sink limitation. In contrast, substantial remobilization of stem dry matter occurred for D2F11 in both years. This indicates a tendency toward a source limitation within the colimitation. The actual photosynthesis was not enough to satisfy the demand of the developing grains, that used, in consequence, part of the stored stem reserves.

The rate and efficiency of the vegetative dry matter remobilization supported the trends to a source or sink limitation shown by the hybrids D2F11 and SPS 240, respectively. The stem CH evolution of the control treatment showed accumulation or light remobilization for SPS 240, and strong remobilization for D2F11. The remobilization rate and efficiency showed similar results.

In both years, the control treatments were away of the maximum possible accumulation (FS) or remobilization (GFS) measured in the experience, indicating the presence of both limitations. However, SPS 240 was closer to the maximum accumulation (sink limitation trend) and D2F11 closer to the maximum possible remobilization observed in the experiment (source limitation trend).

Then, Balcarce presents environmental conditions that place it in an intermediate position with respect to the tropics (that presents a net reproductive sink capacity limitation for grain yield) and Canada (that presents a source limitation).

CONCLUSIONS

The results indicate the existence of a colimitation by source of assimilates and reproductive sinks because grain yield dropped similarly in response to shading during the flowering and the grain filling periods.

FS reduced the grain number/unit area and slightly increased the 1 000 kernel weight. GFS reduced the 1 000 kernel weight, and to a lesser extent, the grain number/unit area.

Shading at any period produced, relative to the control, a decrease in stem CH content during the time of treatment imposition. The FS treatments presented, during the post-shading period, a greater CH accumulation in stems than the control. This is explained by the decrease of reproductive sink number that produced a drop in their demand of CH and by the increased importance of the stem as an alternative sink for assimilates. GFS treatments produced a strong increase in CH remobilization rate from stem during the time of treatment imposition.

The two hybrids did not show statistically significant differences in their source–sink relationships. Nevertheless, a tendency towards a source limitation was evident in the long season hybrid.

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