

# Seed Number as a Function of Growth. A Comparative Study in Soybean, Sunflower, and Maize

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## ABSTRACT

Seed number, the main yield component of cereals and oil-seed species, strongly depends on the physiological status of the crop during a critical period for seed set. Using a comparative approach including three species with contrasting reproductive strategies, we investigated the relationship between seed number per plant (SNP) and plant growth rate during the critical period for seed set ( $PGR_C$ ). Indeterminate soybean [*Glycine max* (L.) Merr.], sunflower (*Helianthus annuus* L.), and maize (*Zea mays* L.) crops were grown under a wide range of plant densities to generate contrasting availability of resources per plant. Growth of individual plants was estimated by a novel, nondestructive method based on relationships between actual shoot dry matter and morphometric variables, including stem diameter, plant height, and dimensions of reproductive structures. Seed number per plant ranged from 0 to 890 in soybean, 0 to 4096 in sunflower, and 0 to 1348 in maize and  $PGR_C$  ( $g\ d^{-1}$ ) from 0.01 to 4.3 in soybean, 0.3 to 17.6 in sunflower, and 0.4 to 12.3 in maize. Our study showed that (i) the relationship between SNP and  $PGR_C$  was linear in soybean, reflecting the reproductive plasticity of this species, and curvilinear in sunflower and maize, reflecting morphogenetic restrictions to generate reproductive sinks under favorable growing conditions; (ii) the  $PGR_C$  threshold below which no seed was set varied among species, being negligible in soybean, close to  $0.35\ g\ d^{-1}$  in sunflower, and  $1\ g\ d^{-1}$  in maize. Quantitative relationships between seed number and plant growth rate during the critical period of seed set could be useful for crop modeling.

SEED NUMBER, the main yield component of cereals and oil-seed crops, is strongly dependent on genotype, environmental and management factors (Egli, 1998). In soybean, sunflower, and maize, seed number depends on the sequential processes of flower morphogenesis and seed set. The former controls potential seed number and has a relatively low energy cost. In general, even in very productive environments, flower number exceeds the potential capacity of plants to set seeds (Stephenson, 1981). In contrast, seed set is very sensitive to the physiological status of crops during critical windows of time that are species dependent. Despite some uncertainty about the actual beginning and the end of this critical period, it is generally accepted that it brackets flowering in maize (Earley et al., 1967; Aluko and Fischer, 1988) and sunflower (Cantagallo et al., 1997). In indeterminate soybean, the critical period for seed set extends from flowering to beginning or middle seed

filling (Board and Tan, 1995; Jiang and Egli, 1995; Egli, 1998).

Growth rate during the window of time critical for seed set has been used to quantify the physiological status of crops as affected by genotype, environment, and their interaction. Further, empirical evidence supports the association between seed number and crop growth (Hawkins and Cooper, 1981; Egli and Yu, 1991). Controversy exists, however, on the actual shape of the relationship between SNP and  $PGR_C$  in maize (Tollenaar et al., 1992; Kiniry et al., 1997; Ritchie and Wei, 2000) and no reports have been found regarding the SNP- $PGR_C$  relationship in sunflower. Importantly, most research related to seed set has dealt with single plant species. In this work, a comparative approach is used to highlight common pathways and contrasts in the way in which seed set is determined in major crop species.

Sunflower, soybean, and maize are three annual species with contrasting reproductive strategies. Our hypothesis is, therefore, that the putative relationship between seed number and plant growth rate during the critical period for seed number determination is not unique but strongly depends on the reproductive strategies of the species. Because plant-to-plant variation is an important feature of plant populations (Hara, 1986), we propose a novel analysis of the SNP- $PGR_C$  relationship at the level of interacting individuals within crops. To assess growth of individuals during the critical period for seed set and relate it to SNP at harvest, we developed an original, nondestructive method to quantify  $PGR_C$ . The study of individual plants under a comparative approach including contrasting species is a powerful tool to improve our understanding of seed number determination.

## MATERIALS AND METHODS

### Crop Management and Treatments

Soybean, sunflower, and maize crops were grown on deep ( $\geq 1.5\ m$ ) Typical Argiudolls at Balcarce, Argentina, ( $37^{\circ}45' S$ ,  $58^{\circ}18' W$ ; elevation 130 m) between 1994 and 1999 (Table 1). All crops were fertilized with  $35\ kg\ P\ ha^{-1}$  before sowing, and with  $150\ kg\ N\ ha^{-1}$  at the 6-leaf stage in maize and 4-leaf stage in sunflower. Soybean seed was inoculated with *Bradyrhizobium japonicum*. Irrigation was provided to keep water content above 50% of maximum soil available water. Weeds and insects were adequately controlled. Each species was grown in a different section of the same field. Plant density treatments were arranged within each crop species in a randomized block design with three (Season I) or four replications (Season II). Distance between rows was 0.7 m in all three species, except for soybean in Season II, when 0.35 m between rows was used. Target plant densities in maize and sunflower (Table 1) were achieved by hand sowing and thinning to one plant per hill. Thickly sown soybean was thinned to the appropriate density at the 2-leaf stage.

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**Table 1. Summary of treatments in field experiments at Balcarce.**

Species	Cultivar	Season (date of emergence)	Plant population plants m <sup>-2</sup>	Number of
				individuals sampled
Soybean	Asgrow 3127	I (13 Nov. 1994)	7.9, 29.8 and 56.5	322
	Asgrow 4100	II (16 Nov. 1998)	2.9 and 30	117
Sunflower	DK G-100	I (27 Oct. 1994)	1.4, 5.8 and 10.3	258
	DK G-100	II (26 Oct. 1997)	1.3, 1.6, 2.0, 3.6, 5.3, 10.2, 14.3 and 17.9	281
Maize	DK 636	I (17 Oct. 1994)	2.2, 8.5 and 16.9	298
	DK 639	II (2 Nov. 1997)	2.0, 3.6, 8.4, 13.0, 15.9 and 20.4	287

### Measurements

Shoot dry matter of individual plants was quantified at the beginning and end of the critical period for seed set. We used a nondestructive method based on allometric relationships between selected plant variables and actual shoot dry matter obtained in conventional plant samplings (see below). Plant samples were taken 15 d before and 15 d after flowering in maize and sunflower. In soybean, samples were taken at full flowering and at the middle of seed filling. Sampling strategies varied between seasons. In the first season, three plant densities were established and large samplings were taken to exploit variation within treatments as well as variation among treatments. In the second, we increased the number of treatments and took fewer plants per treatment (Table 1).

### Allometric Relationships

We measured basal stem diameter and, when visible, diameter and length of ears in maize and head diameter in sunflower. In Season II, stem diameter in soybean was measured at the height of the internode associated with the first trifoliate leaf and the number of branches and height of the main stem were also included as variables. Immediately after taking these measurements, shoots were harvested, separated into leaf blade and petiole, stem and reproductive structures, and oven dried at 65°C to constant weight to determine dry matter. Samples included three plants per replicate at low density and five plants per replicate at high and intermediate densities (Table 2). Relationships between shoot dry matter and morphometric variables were evaluated using regression models summarized in Table 2.

### Plant Growth Rate and Seed Number

We tagged a density-dependent number of plants (Table 1) to determine (i) shoot dry matter at the beginning ( $S_0$ ) and end ( $S_1$ ) of the critical period for seed set, and (ii) seed number at physiological maturity. Shoot dry matter per plant,  $S_0$  and  $S_1$ , was estimated for each plant on the basis of nondestructive measurements and the models in Table 2, and  $PGR_C$  calculated

as  $(S_1 - S_0)/d$  between samplings. In maize and soybean, we counted all the seed on each individual plant. In sunflower, we counted the seed in subsamples from about a quarter of the head and estimated total seed number as a function of total seed mass and the ratio between seed number and mass from the subsamples. In maize, the number of fertile ears per plant was also recorded.

We investigated the relationship between SNP and  $PGR_C$  using linear and nonlinear models. In maize and sunflower, several nonlinear functions adequately fitted the data (Andrade et al., 1999). Of them, we chose hyperbolic functions because they are statistically sound and include biologically meaningful parameters (Edmeades and Daynard, 1979; Tollenaar et al., 1992; Vega et al., 2000). The selected models were as follows.

For soybean,

$$SNP = \alpha_1 + \beta_1 PGR_C \quad \text{Model 1}$$

For sunflower and maize,

$$SNP = \frac{\alpha_2(PGR_C - G_T)}{1 + \beta_2(PGR_C - G_T)} \quad \text{for } PGR_C > G_T$$

Model 2

In Model 2,  $G_T$  is the growth rate threshold for seed set. In Model 1, the threshold is calculated as  $-\alpha_1 \beta_1^{-1}$ . For comparisons among species,  $G_T$  was normalized by expressing it as a fraction of average  $PGR_C$  at the most common plant density in commercial crops, i.e., 30 plants m<sup>-2</sup> in soybean, 5.6 plants m<sup>-2</sup> in sunflower, and 8.5 plants m<sup>-2</sup> in maize. In soybean, normalized  $G_T$  was calculated on the basis of the average  $PGR_C$  measured in sterile plants. Parameters  $\alpha_2$  and  $\beta_2$  are defined in Table 3.

Additionally, we calculated independent estimates of SNP and  $PGR_C$  on the basis of averages (hereafter referred as conventional plant sampling). Average plant growth rate during the critical period was assessed as the quotient between crop growth rate and plant density. Samples to determine crop growth rate ( $g d^{-1} m^{-2}$ ) were taken at the beginning and at the end of the critical period; consisted of three (low density)

**Table 2. Relationships between shoot dry matter (S) and morphometric variables. Subscripts 0 and 1 indicate the beginning and the end of the critical period for seed set, respectively. SD: stem diameter; HD: head diameter; ED: diameter of apical ear; EL: length of the apical ear; BN: branch number; H: stem length. All models were significant at  $P < 0.0001$ .**

Species	Season	Model	R <sup>2</sup>	n
Soybean	I	$S_0 = 0.5 + 21.624 SD^{2.27}$	0.78	106
		$S_1 = 2.80 - 18.84 SD + 72.76 SD^2$	0.81	110
	II	$S_0 = 16.48 SD^{2.36} + 1.99E-07 (BN+H)^{4.68}$	0.95	45
		$S_1 = 1.87 + 56.94 SD^{3.05} + 0.76 BN^{1.90}$	0.99	39
Sunflower	I	$S_0 = -13.34 + 11.84 SD^2$	0.93	54
		$S_1 = 5.00 + 8.06 SD^2 + 0.28 HD^2$	0.95	54
	II	$S_0 = 8.38 SD^{2.56} + 0.06 HD^{2.50}$	0.92	84
		$S_1 = 1.86 + 11.11 SD^{2.43} + 0.08 HD^{2.15}$	0.96	104
Maize	I	$S_0 = 19.43 + 4.45 SD^2$	0.75	52
		$S_1 = 31.09 + 7.12 SD^{2.50} + 0.12 (ED EL)^{1.25}$	0.95	54
	II	$S_0 = 11.68 SD^{2.02}$	0.85	111
		$S_1 = 21.21 + 7.12 SD^{2.52} + 0.22 (ED EL)^{1.25}$	0.93	127

**Table 3. Parameters ( $\pm$  s.e.) of Model 2 fitted to seed number per plant (SNP) and plant growth rate during the critical period for seed set (PGR<sub>C</sub>) in individuals of sunflower and maize.**

Species	Season	$\alpha_2$	$G_T$ (g d <sup>-1</sup> )	$\beta_2$	$R^2$ †
Sunflower	I	863.6 $\pm$ 61.13	0.39 $\pm$ 0.102	0.21 $\pm$ 0.022	0.84
	II	1049.6 $\pm$ 72.35	0.31 $\pm$ 0.075	0.25 $\pm$ 0.029	0.82
Maize‡	I	631.8 $\pm$ 49.58	1.02 $\pm$ 0.057	0.96 $\pm$ 0.091	0.72
	II	593.3 $\pm$ 61.26	0.91 $\pm$ 0.073	0.66 $\pm$ 0.098	0.73

Parameters are:  $\alpha_2$  (initial slope),  $G_T$  (PGR<sub>C</sub> threshold for seed set), and  $\beta_2$  (slope at high values of PGR<sub>C</sub>). All regressions and parameters were significant at  $P < 0.0001$ .

† Coefficient of determination.

‡ The fitted model did not include seed from the second ear in prolific plants.

or five plants (high and intermediate densities) in sunflower and maize and 1-m row in soybean and were processed as described above. At physiological maturity, grain yield was estimated by harvesting 7 m<sup>2</sup> (soybean) and 10 m<sup>2</sup> (sunflower and maize). Weight per seed was determined in two 500-seed samples per replicate. Seed number per plant was estimated as the quotient between yield and weight per seed and plant density.

### Potential Seed Number per Plant

Average potential seed number per plant (PSNP) was determined for each plant density treatment and crop in Season I. In sunflower, PSNP was estimated as the sum of filled seeds, empty seeds, and sterile florets. In maize, PSNP of the uppermost ear was calculated as the sum of numbers of kernels and infertile florets. In sunflower and maize, we took two to three plants per replicate. In soybean, total number of flowers was estimated on the basis of periodic flower counts of 10 randomly selected and tagged individual plants. The PSNP in soybean was calculated as the product of total number of flowers and average number of seeds per pod. The fertility ratio was defined as  $SNP \text{ PSNP}^{-1}$ .

## RESULTS

### Estimates of Shoot Dry Matter

Morphometric variables accounted for most of the variation in shoot dry matter (Table 2). The relationship between shoot dry matter and morphometric variables was stronger at the end of the critical period of grain set, when both stem diameter and size of reproductive structures were used as independent variables, than at the beginning, when only stem diameter was used. In soybean, measurement of stem diameter at the height of the second internode and the inclusion of branch number significantly improved the  $R^2$  in Season II. The strong association between actual shoot dry matter at physiological maturity and shoot dry matter estimated with morphometric variables during the critical period further supports the reliability of the method ( $0.79 < r^2 < 0.94$ ;  $P < 0.0001$ ).

### Relationship between SNP and PGR<sub>C</sub> on the Basis of Averages

Figure 1 shows the relationship between average plant growth rate and average seed number per plant in Season I and compares plant growth rate calculated with estimated and actual shoot dry matter (conventional plant sampling) at the beginning and the end of the critical period for seed set. The agreement between these two independent methods to estimate SNP and

PGR<sub>C</sub> reinforces the reliability of our nondestructive approach.

Data based on individual plants allowed us to analyze plant-to-plant variation. In all three species, the coefficient of variation (CV) of both PGR<sub>C</sub> and SNP increased with plant density (Fig. 2). Variation in PGR<sub>C</sub> was greatest in soybean and lowest in maize. In soybean and sunflower, variation in seed number paralleled the variation in plant growth rate. In contrast, maize plants at the lowest and highest densities showed larger variation in seed number than in plant growth rate.

### Relationship between SNP and PGR<sub>C</sub> on the Basis of Individuals

Data from individual plants showed a wide range of both plant growth rate and seed number (Fig. 3). Plant growth rates (g d<sup>-1</sup>) varied between 0.01 and 4.3 in soybean; 0.3 and 17.6 in sunflower, and 0.4 and 12.3 in maize. Seed number per plant ranged from 0 to 890 in soybean, 0 to 4096 in sunflower, and 0 to 1348 in maize.

In all three species, the number of seeds set by each individual was closely associated with its growth rate during the critical period. The relationship between SNP and PGR<sub>C</sub> was best described by a linear model in soybean and by hyperbolic models in sunflower and maize (Fig. 3, Tables 3 and 4). In maize, the model was fitted to SNP for the uppermost ear in prolific and nonprolific plants. In soybean, nonlinear models had slightly higher  $R^2$  but poorer distribution of residuals than the linear models in Table 4. In sunflower and maize, the relationship between SNP and PGR<sub>C</sub> revealed significant PGR<sub>C</sub> thresholds for seed set ( $G_T$ ). These thresholds were close to 0.35 g d<sup>-1</sup> in sunflower and close to 1 g d<sup>-1</sup> in maize ( $P < 0.0001$ ; Table 3). In contrast, the threshold in soybean was not significantly different from zero (Table 4). Moreover, calculated thresholds were negative, a biologically meaningless result which would imply the setting of seed in plants with zero growth rate. Clearly, statistics did not have enough resolution to detect growth thresholds in soybean.

Average PGR<sub>C</sub> in plants without seeds were 0.08  $\pm$  0.067 (Season I) and 0.01  $\pm$  0.006 (Season II) g d<sup>-1</sup> in soybean, 0.49  $\pm$  0.044 (Season I) and 0.25  $\pm$  0.052 (Season II) g d<sup>-1</sup> in sunflower, and 1.11  $\pm$  0.460 (Season I) and 1.02  $\pm$  0.200 (Season II) g d<sup>-1</sup> in maize. These values correlated with reported  $G_T$  in Table 3. Normalized thresholds to account for differences in plant growth rate among species ranked soybean ( $8.8 \pm 5.63$ ) < sunflower ( $11.0 \pm 2.84$ ) < maize ( $25.8 \pm 1.76$ ) (average for

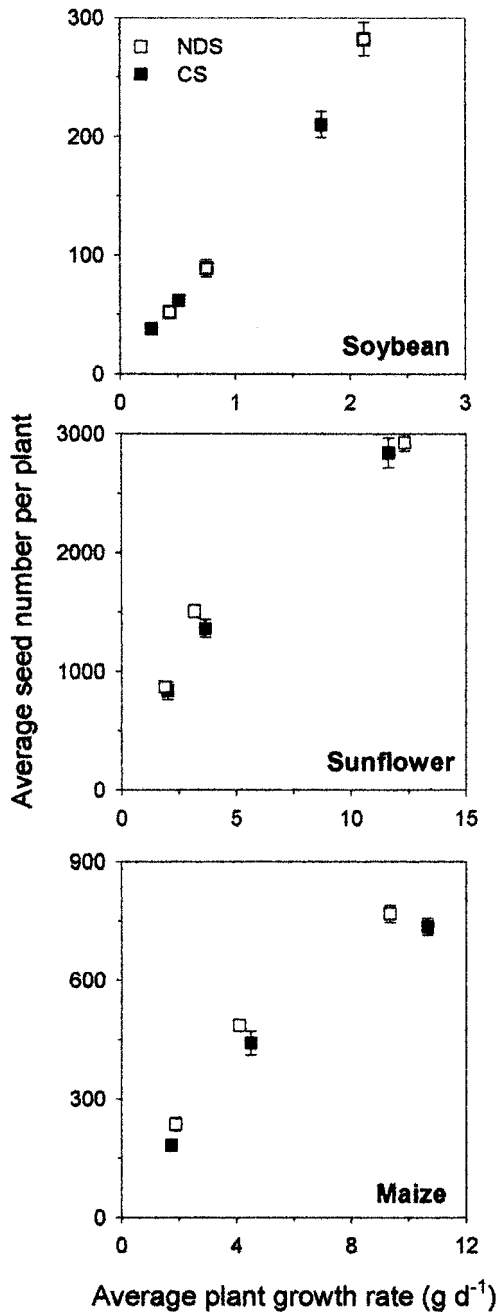


Fig. 1. Relationship between average seed number per plant at maturity and average plant growth rate during the critical period for seed set in Season I. Data obtained from nondestructive measurements (NDS) and from conventional plant sampling (CS). In maize, seed number per plant includes seeds in the uppermost and in the subapical ear. Bars indicate standard error of the mean.

two seasons). Maize presented the highest  $G_T$  and the largest proportion of sterile plants at high density, i.e., 26% compared with 7% in sunflower and 3% in soybean (values for Season I).

For hybrids used in this work, SNP did not significantly increase when  $PGR_C$  was greater than 4 g d<sup>-1</sup> in maize (considering the uppermost ear only) or 7 g d<sup>-1</sup> in sunflower. This indicated a restriction in reproductive output that was not observed in soybean (Fig. 3).

Some maize plants produced a second seed-bearing

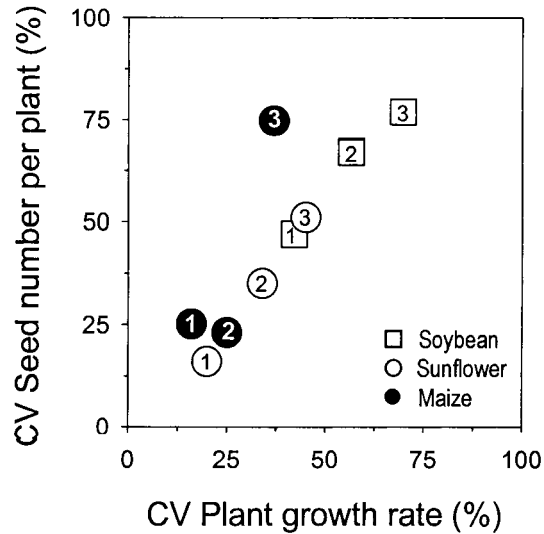


Fig. 2. Coefficient of variation of average seed number per plant at maturity and average plant growth rate during the critical period for seed set as a function of plant density in Season I. Number 2 indicates commercial densities (29.8, 5.8, and 8.5 in soybean, sunflower and, maize, respectively). Numbers 1 and 3 indicate low and high densities, respectively (Table 1).

ear (Fig. 3). Growth thresholds for prolificacy were close to 6 g d<sup>-1</sup> in Season I (DK 636) and to 5 g d<sup>-1</sup> in Season II (DK 639). In both seasons, about 50% of plants that grew at  $PGR_C$  greater than the threshold for prolificacy set a second fertile ear.

Average potential seed number per plant (PSNP) decreased 70% in soybean, 50% in sunflower, and 11% in maize from low to high density. The fall in  $PGR_C$  associated with increasing plant density decreased the fertility ratio,  $SNP \text{ PSNP}^{-1}$ , from 0.74 to 0.44 in soybean, from 0.80 to 0.47 in sunflower and from 0.93 to 0.26 in maize.

## DISCUSSION

### Analysis of Individuals within Plant Communities

We developed a reliable method based on the combination of nondestructive and destructive plant sampling to estimate the growth rate of individual plants during the critical period for seed set (Table 2; Fig. 1). This approach allowed for (i) the investigation of the relationship between SNP and  $PGR_C$  within ranges of  $PGR_C$  and SNP much larger than the usually obtained with standard methods based on average plants (cf. Fig. 2 with Fig. 3) and (ii) the analysis of plant-to-plant variation.

Plant-to-plant variation of both growth rate and reproductive output was greatest in soybean, whereas variation in growth rate at intermediate and low plant densities was greater in sunflower than in maize (Fig. 2). This reflected a differential development of exploitation hierarchies for resources among individuals (Hara, 1986). A number of factors contribute to these differences: first, the greater extinction coefficient and the greater phenotypic plasticity of sunflower and soybean (Andrade et al., 2000) in relation to maize, a species with more erect leaves (Hara, 1986); second, a relatively earlier interaction among individuals in soybean owing



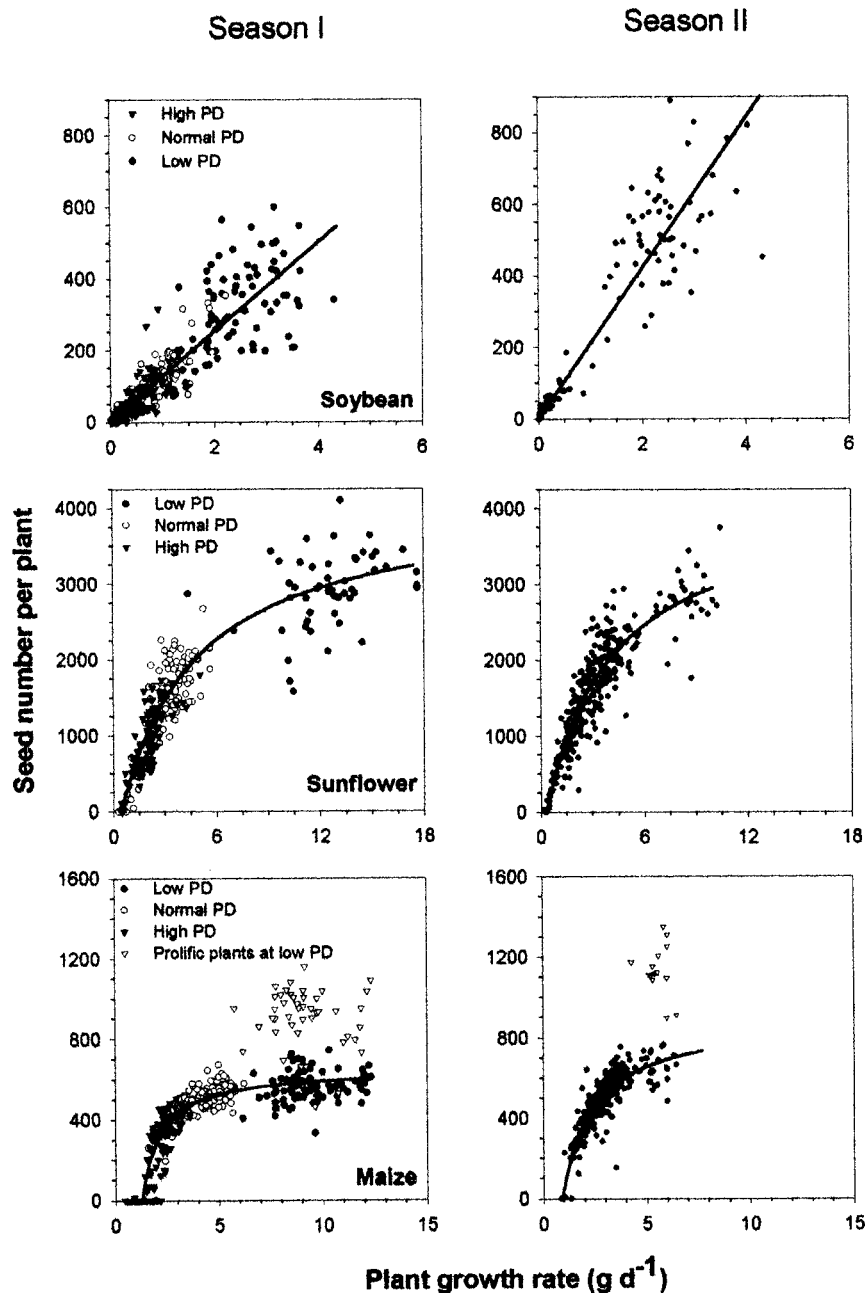


Fig. 3. Seed number per plant and plant growth rate during the critical period for seed set in soybean, sunflower, and maize individuals during two growing seasons at Balcarce. In Season I, symbols indicate plant densities (PD). Normal densities (D) were 29.8, 5.8, and 8.5  $\text{p m}^{-2}$  in soybean, sunflower, and maize, respectively. Low PD was 0.25D and high PD was 2D. In maize, each point represents seed number in the uppermost ear of nonprolific and prolific plants, except when otherwise indicated. In maize, the fitted curve did not include seed from the second ear in prolific plants. Parameters of the fitted relationships are in Table 3.

to the comparatively higher plant density; third, the greater foraging capacity for light and nutrients in dicots than in monocots, derived from both shoot and root morphological features (Grime, 1988).

Increasing interference among neighboring plants increased the coefficient of variation of both SNP and  $\text{PGR}_C$  in all three crops. In maize, at the highest density, however, the coefficient of variation was much greater for seed number than for growth rate; this was associated with a bimodal frequency distribution of SNP resulting from a large number of barren plants (data not shown). In soybean and sunflower, self thinning of the

smallest plants may explain lack of comparable barrenness and bimodality in SNP (Hara, 1986; Vega, 1995, unpublished data). Most importantly, however, differences in barrenness among species were associated with differences in  $\text{PGR}_C$  thresholds for seed set.

#### The Relationship between $\text{PGR}_C$ and SNP. Meaning and Applications

Notwithstanding the contrasting reproductive strategies of sunflower, soybean, and maize, the relationship between SNP and  $\text{PGR}_C$  held for all three species (Fig 3; tables 3 and 4). The consistency of this highlights the

**Table 4. Parameters ( $\pm$  s.e.) of the linear Model 1 fitted to seed number per plant (SNP) and plant growth rate during the critical period for seed set ( $PGR_C$ ) for individuals of soybean. Regressions were significant at  $P < 0.0001$ .**

Season	$\alpha_1$	$\beta_1$	$R^2$ ‡
I	4.5 $\pm$ 5.34NS	123.9 $\pm$ 3.77†	0.77
II	23.7 $\pm$ 13.30NS	199.7 $\pm$ 7.65†	0.86

† Significant at  $P \leq 0.0001$ ; NS, not significant.

‡ Coefficient of determination.

value of  $PGR_C$  as a variable that synthesizes the key determinants of seed set. Because of its role as an energy source in plants, carbon tends to integrate the allocation patterns of other resources and can therefore be used as a common currency (Reekie and Bazzaz, 1987; Egli, 1998). The relationship between SNP and  $PGR_C$ , however, should not be taken as an indication of a causal effect. Importantly, factors other than carbohydrate availability, including mineral nutrients (Swank et al., 1982), water deficit (Westgate, 1994), and growth regulators (Carlson et al., 1987), can concurrently influence seed set. The SNP- $PGR_C$  relationship showed to be, however, useful in this comparison of species with contrasting reproductive strategies and may help understand environmental and genotype-related variation in seed set within a species (Tollenaar et al., 1992; Jiang and Egli, 1995; Echarte et al., 1998). It also may provide a method to estimate seed number in simulation models.

### Comparative Physiology of Seed Number Determination

Our study showed that there is (i) a growth rate threshold during the critical period for seed set below which no seed is set, (ii) a substantial variation in this threshold among species, and (iii) a differential reproductive plasticity in response to increasing  $PGR_C$  among species.

Thresholds of biomass per plant for reproduction have been described in the literature (Gardner and Gardner, 1983; Weiner, 1988; Vega et al., 2000). Interpretation of such thresholds, however, may be misleading as they are measured at harvest and are not necessarily associated with the actual situation of growth of plants during the critical period for seed set. In species as maize, for example, biomass accumulation in stems of barren plants continue during a relatively long period until photosynthesis is feed-back regulated (Dalla Valle, 1998). Growth thresholds during critical periods for seed set, hence, are more meaningful for understanding seed number determination; however, they have been scarcely mentioned and mostly in maize (Edmeades and Daynard, 1979; Tollenaar et al., 1992). Controversy, moreover, still remains regarding the existence of such growth thresholds for seed set (Tollenaar et al., 1992; Kiniry et al., 1997; Ritchie and Wei, 2000). We consider that no discussion about thresholds in this type of relationships is the result of lack or shortage of data at very low values of  $PGR_C$ . In our work, the use of individuals, rather than average plants representing a treatment, allowed us to get a very ample range of  $PGR_C$  and an adequate calculation of  $G_T$ .

Maize showed the highest  $G_T$  for seed set, reflecting

significant reductions of dry matter allocation to reproductive structures and developing kernels under conditions of low growth (Edmeades et al., 1979; Andrade et al., 1999). This may result from hierarchical patterns of distribution of assimilates within the plant (Edmeades et al., 1979). Stressful conditions during the critical period for seed set affect growth of ears and silks more than growth of other organs in maize (Hall et al., 1982; Otegui, 1997). In contrast, intermediate  $G_T$  in sunflower and low  $G_T$  in soybean may reflect a comparatively earlier and more stable allocation of dry matter to reproductive structures even under poor growing conditions.

Differences in abortion among species may additionally be related to other aspects of the floral biology, as the degree of synchrony in the pollination of florets, development of young seed, and the outcome of hierarchies among reproductive sinks (Stephenson, 1981; Bangerth, 1989; Lafitte and Edmeades, 1995). If flowers and young fruits compete for limited maternal resources, the proportion of pollinated flowers that set fruit decreases as the number of pollinated flowers increases (Stephenson, 1981). In comparison with sunflower and maize, soybean seems to adjust the potential number of reproductive sinks in an apparent balance with the availability of assimilates in the plant. Contrasting, poor growing conditions have comparatively little effect on the number of potential florets in maize (Ruget and Duburcq, 1983; Otegui, 1997). Hence, competition for limited assimilates among simultaneously developing seeds would be more accentuated in maize.

With increasing availability of resources and hence, plant growth, the relationship between SNP and  $PGR_C$  tended to be linear in indeterminate soybean and curvilinear in sunflower and maize. Indeterminate soybean has a greater reproductive plasticity in response to increasing availability of resources than determinate plants with no (sunflower) or limited (maize) capacity to adjust the number of fertile reproductive sites (Loomis and Connor, 1996). In soybean, this plasticity reflects both a reproductive strategy primarily based on a pattern of allocation of meristems favoring branching and reproduction and a low dominance for assimilates among reproductive sites (Bonser and Aarssen, 1996; Sadras, 2000). A long critical period and a very marked modular structure, i.e., the production of rather independent metameric units that consist of a node-internode, functional racemes, and subtending leaf evenly distributed within the canopy, can account for a finer tuning between plant growth and setting of seed in soybean.

In contrast, the curvilinear relationships between SNP and  $PGR_C$  for sunflower and for the uppermost ear in maize reflect a ceiling in reproductive plasticity. Strong apical dominance in maize and sunflower implies limited allocation to branch reproductive meristems (Sadras, 2000) despite the potential of maize plants to produce many ears. Lack of additional reproductive sinks may set more severe limitations to yield per plant, however, in nontillering and nonprolific maize than in sunflower because the latter has a greater ability to adjust flower and seed number per inflorescence and seed mass (Vega et al., 2000). In maize then, ear plasticity, prolificacy,

and the threshold  $PGR_C$  to set kernels in the second ear are features that correlate with a higher efficiency in  $SNP PGR_C^{-1}$  in favorable environments. These features, nevertheless, are largely influenced by genetic and environmental factors (Otegui, 1995; Echarte et al., 1998).

## CONCLUSION

Consideration of interacting among individual plants within crops allowed us to develop strong relationships between seed number and growth rate during the critical period for seed set in species of contrasting growth habit, morphology, and physiology. Growth thresholds for seed set ranked soybean < sunflower < maize. The relationship between SNP and  $PGR_C$  was linear in soybean, reflecting the high reproductive plasticity of this species, and curvilinear in sunflower and maize, reflecting ceilings in reproductive plasticity associated with morphogenetic restrictions in the production of additional reproductive sinks under favorable growing conditions. Prolific maize plants set more seed per unit  $PGR_C$  than did nonprolific plants, highlighting the value of prolificacy for the adjustment to variable environments.

## REFERENCES

- Aluko, G.K., and K.S. Fischer. 1988. The effect of changes of assimilate supply around flowering on grain sink size and yield of maize (*Zea mays* L.) cultivars of tropical and temperate adaptation. *Aust. J. Agric. Res.* 39:153-161.
- Andrade, F.H., L.A.N. Aguirrezabal, and R.H. Rizzali. 2000. Crecimiento y rendimiento comparados. p. 61-96. *In* F.H. Andrade and V.O. Sadras (ed.) Bases para el manejo del maíz, el girasol y la soja. INTA-FCA (UNMDP), Balcarce, Argentina.
- Andrade, F.H., C.R. Vega, S.A. Uhart, A.G. Cirilo, M. Cantarero, and O. Valentinuz. 1999. Kernel number determination in maize. *Crop Sci.* 39:453-459.
- Bangerth, F. 1989. Dominance among fruits/sinks and the search for a correlative signal. *Physiol. Plant.* 76:608-614.
- Board, J.E., and Q. Tan. 1995. Assimilatory capacity effects on soybean yield components and pod number. *Crop Sci.* 35:846-851.
- Bonser, S.P., and L.W. Aarssen. 1996. Meristem allocation: a new classification theory for adaptive strategies in herbaceous plants. *Oikos* 77:347-352.
- Cantagallo, J.E., C.A. Chimenti, and A.J. Hall. 1997. Number of seeds per unit area in Sunflower correlates well with a photothermal quotient. *Crop Sci.* 37:1780-1786.
- Carlson, D.R., D.J. Dyer, C.D. Cotterman, and R.C. Durley. 1987. The physiological basis for cytokinin induced increases in pod set in IX93-100 soybeans. *Plant Physiol.* 84:233-234.
- Dalla Valle, D.E. 1998. Rendimiento y calidad de silaje de maíz en función del número de granos fijados. M.S. Thesis-Universidad Nacional de Mar del Plata, Balcarce, Argentina.
- Earley, E.B., W.O. McIlrath, R.D. Seif, and R.H. Hageman. 1967. Effects of shade applied at different stages on corn (*Zea mays* L.) production. *Crop Sci.* 7:151-156.
- Echarte, L., C.R. Vega, F.H. Andrade, and S. A. Uhart. 1998. Kernel number determination in Argentinian maize hybrids released during the last three decades. p. 102-103. *In* M.E. Otegui and G.A. Slafer (ed.) Proc. International Workshop on Physiological basis for Maize improvement, 1st, Bs. As., Argentina. 8-9 Oct. 1998. Escuela para Graduados, Fac. Agron. Universidad de Buenos Aires, Buenos Aires, Argentina.
- Edmeades, G.O., and T.B. Daynard. 1979. The relationship between final yield and photosynthesis at flowering in individual maize plants. *Can. J. Plant Sci.* 89:585-601.
- Edmeades, G.O., N.A. Fairey, and T.B. Daynard. 1979. Influence of plant density on the distribution of C-labelled assimilate in maize at flowering. *Can. J. Plant Sci.* 59:577-584.
- Egli, D.B. 1998. Seed biology and the yield of grain crops. 1st ed. CAB International, Oxford, UK.
- Egli, D.B., and Z. Yu. 1991. Crop growth rate and seeds per unit area in soybean. *Crop Sci.* 31:439-442.
- Gardner, W.R., and H.R. Gardner. 1983. Principles of water management under drought conditions. *Agric. Water Manag.* 7:143-155.
- Grime, J.P. 1988. Annual Report 1996-1998. Unit of Comparative Plant Ecology, The University of Sheffield, Sheffield, UK.
- Hall, A.J., F. Villela, N. Trapani, and C.A. Chimenti. 1982. The effect of water stress and genotype on the dynamics of pollen shedding and silking in maize. *Field Crops Res.* 5:349-363.
- Hara, T. 1986. Effects of density and extinction coefficient on size variability in plant populations. *Ann. Bot. (London)* 57:885-892.
- Hawkins, R.C., and P.J. Cooper. 1981. Growth, development and grain yield of maize. *Expl. Agric.* 17:203-207.
- Jiang, H., and D.B. Egli. 1995. Soybean seed number and crop growth rate during flowering. *Agron. J.* 87:264-267.
- Kiniry, J.R., J.R. Williams, R.L. Vanderlip, J.D. Atwood, D.C. Reicosky, J. Mulliken, W.J. Cox, H.J.J. Mascagni, S.E. Hollinger, and W.J. Wiebold. 1997. Evaluation of two maize models for nine U.S. locations. *Agron. J.* 89:421-426.
- Lafitte, H.R., and G.O. Edmeades. 1995. Stress tolerance in tropical maize is linked to constitutive changes in ear growth characteristics. *Crop Sci.* 35:820-826.
- Loomis, R.S., and D.J. Connor. 1996. Crop Ecology. Productivity and Management in Agricultural Systems. 1st ed. Cambridge University Press, Cambridge, UK.
- Otegui, M.E. 1995. Prolificacy and grain yield components in modern argentinian maize hybrids. *Maydica* 40:371-376.
- Otegui, M.E. 1997. Kernel set and flower synchrony within the ear of Maize: II. Plant population effects. *Crop Sci.* 37:448-455.
- Reekie, E.G., and F.A. Bazzaz. 1987. Reproductive effort in plants. 2. Does C reflect the allocation of other resources? *Am. Nat.* 129:897-906.
- Ritchie, J.T., and J. Wei. 2000. Models of kernel number in maize. p. 75-88. *In* M.E. Westgate and K.J. Boote (ed.) Physiology and modeling kernel set in maize. ASA, Madison, WI.
- Ruget, F., and J.B. Duburcq. 1983. Développement reproducteur des bourgeons axillaires chez le maïs: stades de différenciation, nombre du fleurs. *Agronomie* 3:797-808.
- Sadras, V.O. 2000. Variation in apical dominance and its implications for herbivory resistance, competitive ability and biomass partitioning. p. 139-156. *In* M.E. Otegui and G.A. Slafer (ed.) Physiological basis for maize improvement. Food Products Press, The Haworth Press, Binghamton, NY.
- Stephenson, A.G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annu. Rev. Ecol. Syst.* 12:253-279.
- Swank, J.C., F.E. Below, R.J. Lambert, and R.H. Hageman. 1982. Interaction of carbon and nitrogen metabolism in the productivity of maize. *Plant Physiol.* 70:1185-1190.
- Tollenaar, M., L.M. Dywer, and D.W. Stewart. 1992. Ear and kernel formation in maize hybrids representing three decades of grain yield improvement in Ontario. *Crop Sci.* 32:432-438.
- Vega, C.R.C., V.O. Sadras, F.H. Andrade, and S.A. Uhart. 2000. Reproductive allometry in Soybean, Maize and Sunflower. *Ann. Bot. (London)* 85:461-468.
- Weiner, J. 1988. The influence of competition on plant reproduction. p. 228-245. *In* J.L. Doust and L.L. Doust (ed.) Plant reproductive ecology: patterns and strategies. Oxford University Press, New York.
- Westgate, M.E. 1994. Seed formation in maize during drought. p. 361-364. *In* K.J. Boote et al. (ed.) Physiology and determination of crop yield. ASA, CSSA, SSSA, Madison, WI.