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Reproductive partitioning and seed set efficiency in soybean, sunflower and maize

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Abstract

Seed number per plant (SNP) can be modelled as a function of plant growth rate during the critical period for seed set ($\mathrm{PGR_C}$), the proportion of plant growth partitioned to reproductive organs (P_R) and the minimum assimilate requirement per seed (λ). In comparison to $\mathrm{PGR_C}$, less attention has been given to P_R and λ. In this paper, we analysed reproductive partitioning and λ in three species of contrasting reproductive strategies, soybean (*Glycine max* L. Merrill), sunflower (*Helianthus annuus* L.) and maize (*Zea mays* L.). To study plant-to-plant variation and to characterise stability of the variables analysed, we focused on individual plants grown under a wide range of plant densities. In soybean and sunflower, reproductive partitioning comprised about 50% of shoot growth, was fairly stable in a wide range of plant growth, and only decreased in a few, very small plants. In comparison, reproductive partitioning in non-prolific maize showed an optimum, was generally below 50% and exhibited a strong variation and instability at plant growth rates $\cong$2 g/day. Among species, stability of reproductive partitioning correlated inversely with a $\mathrm{PGR_C}$ threshold for reproductive growth and positively with reproductive plasticity at high $\mathrm{PGR_C}$. Consideration of reproductive partitioning improved estimation of seed number, particularly in maize, a species prone to barrenness. Seed number as a function of reproductive growth was adequately described through linear (soybean) and hyperbolic models with *x*-intercepts (sunflower and maize). Seed set efficiency in terms of seed number per unit of reproductive growth (Ef) was constant only in soybean. In sunflower and maize, Ef increased with decreasing reproductive growth and became highly variable and unstable when reproductive growth was close to the threshold for seed set. In maize, such threshold was higher than in soybean and sunflower possibly as a consequence of a higher minimum combined demand for assimilate, resulting from a higher λ and number of simultaneously developing sinks. Inclusion of parameters assessing (i) stability in reproductive partitioning at low plant growth rates, and (ii) the minimum assimilate requirement per seed might improve seed number estimation. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Allometry; Reproductive partitioning; Assimilate requirement; Plant-to-plant variation; Plant growth rate; Stability; Seed set efficiency

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1. Introduction

Seed number, the main yield component in cereals and oilseed crops (Shibles et al., 1975; Cantagallo et al., 1997) is closely associated with crop growth rate during the critical period for seed set (Egli and Zhen-wen, 1991; Villalobos et al., 1992). Vega et al. (2001) showed that differences in reproductive strategies among species influenced the relationship between seed number per plant (SNP) and plant growth rate during the critical period for seed set ($\mathrm{PGR_C}$). This relationship was linear in soybean and curvilinear in sunflower and maize. Their study also showed that

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there was a PGR_C threshold for seed set which ranked soybean < sunflower < maize. Thresholds for seed set and non-linearity in the SNP–PGR_C relationship suggested that factors other than PGR_C influenced seed number, including biomass partitioning to reproductive structures and minimum requirements of assimilate to sustain activity of meristems (Charles-Edwards, 1984).

Based on the response of grain legumes to plant density, shading and thinning, Charles-Edwards (1984) proposed that each reproductive structure requires a minimum rate of assimilate supply during its initial development to sustain growth. Several authors have further explored this model, particularly in soybean (Charles-Edwards et al., 1986; Egli and Zhen-wen, 1991; Egli, 1998; Ball et al., 2000). For our purpose, the model can be written as

$$\mathrm{SNP} = \mathrm{PGR_C} P_\mathrm{R} \lambda^{-1} \quad (1)$$

where P_R is the proportion of PGR_C partitioned to reproductive organs and λ is the minimum assimilate requirement per seed. All three independent variables are defined for the most critical period of seed set (Aluko and Fischer, 1988; Board and Tan, 1995; Cantagallo et al., 1997). Ample research on the first factor in Eq. (1) (Edmeades and Daynard, 1979b; Egli and Zhen-wen, 1991; Andrade et al., 1999) emphasises the role of carbon as an energy source and its adequacy to integrate effects of other resources (Gifford et al., 1984). The other factors, P_R and λ, have received less attention. Even though partitioning of biomass to seed is important to yield improvement of most grain and oilseed crops (Slafer, 1994; López Pereira et al., 2000), its physiological regulation is poorly understood (Evans, 1994; Connor and Hall, 1997). The minimum assimilate requirement per seed is particularly difficult to quantify. As a first approach, Egli and Zhen-wen (1991) used the individual seed growth rate to estimate λ in soybean.

Considering that reproductive growth rate, $\mathrm{RepGR_C} = \mathrm{PGR_C} P_\mathrm{R}$, Eq. (1) predicts a linear relationship between SNP and $RepGR_C$, with slope $= \lambda^{-1}$ and intercept $= 0$. The model, hence, would be unrealistic in cases of species with restrictions in sink morphogenesis and/or non-zero thresholds of $RepGR_C$ for seed set.

We investigate seed number determination with emphasis on reproductive partitioning and the minimum assimilate requirement per seed. Soybean, sunflower and maize are compared focusing on individual plants within a crop rather than on the average plant. This approach allows us to study plant-to-plant variation and to characterise stability of the variables analysed.

2. Materials and methods

2.1. Crop management and treatments

Sunflower, maize and indeterminate soybean crops were grown at Balcarce, Argentina (37°45′S, 58°18′W) during two growing seasons. For each species grown in a different section of the same field, plant density treatments were laid out in three (Season I) or four (Season II) randomised blocks (Table 1). All plots were hand-sowed and thinned to one plant per hill. Experiments were conducted under no water or nutrient stress, and pests and weeds were adequately controlled.

Table 1
Summary of treatments in field experiments at Balcarce

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

[a] Number of tagged individuals for non-destructive measurements.

2.2. Measurements

The critical period for seed number determination was considered as 24–30 days bracketing flowering in maize (Earley et al., 1967; Aluko and Fischer, 1988) and sunflower (Cantagallo et al., 1997) and from flowering to full seed (≅65% final dry weight of seeds) in soybean (Board and Tan, 1995; Jiang and Egli, 1995). Shoot and reproductive biomass of tagged plants was quantified at the beginning and end of the critical period using destructive and non-destructive samplings (see below). At full maturity, we determined SNP. In maize, seed number was determined in the apical and subapical ears.

2.3. Destructive samplings

Morphometric variables (number of branches, plant height, length and/or diameter of maize ear and sunflower head) were measured on a density-dependent number of plants, i.e., three plants per replicate at low plant density and 5–8 plants per replicate at high plant densities. Immediately after measurements, plants were harvested, separated into leaf blade, stem plus petiole (sunflower and soybean) or stem plus sheath (maize) and reproductive structures and oven dried at 65°C. Allometric relationships were established between morphometric variables and actual biomass. Models fitted for shoot biomass ($0.75 < R^2 < 0.99$) were presented elsewhere (Vega et al., 2001). Models fitted to reproductive biomass are summarised in Table 2. Reproductive structures included husk, cob and seed in maize, head and seed in sunflower, and pod and seed in soybean.

2.4. Non-destructive samplings

In non-destructive samplings, shoot and reproductive biomass were assessed in tagged individual plants using the allometric relationships shown in Vega et al. (2001) and in Table 2. Strategies for non-destructive sampling varied between seasons. In the first season, three plant population densities were established and a large number of individuals were taken to exploit variation within treatments as well as variation among treatments. In the second season, we increased the number of treatments to 4–7 and took fewer individuals per treatment (Table 1). Growth rate during the critical period was calculated as the ratio between accumulated biomass in shoots or reproductive structures and the duration of the period, assuming reproductive biomass to be negligible at the beginning of the critical period.

2.5. Data analysis

We investigated the relationship between reproductive and plant growth rate and between SNP and reproductive growth rate using linear and hyperbolic functions (Eq. (2)) (Edmeades and Daynard, 1979b; Tollenaar et al., 1992; Vega, 2001):

$$y = \frac{\alpha(x - x_0)}{1 + \beta(x - x_0)} \quad \text{for } x > x_0 \qquad (2)$$

Table 2
Relationships between biomass of reproductive structures (R) and morphometric variables for individual plants of soybean, sunflower and maize[a]

Species	Season	Model	R^2	N[b]
Soybean	I	$R = -2.08 + 26.53\,\mathrm{SD}^{1.98}$	0.70	110
	II	$R = 30.34\,\mathrm{SD}^{2.77} + 0.11\,\mathrm{BN}^{2.80}$	0.99	39
Sunflower	I	$R = 0.15\,\mathrm{HD}^{1.99}$	0.93	54
	II	$R = 0.86 + 0.08\,\mathrm{HD}^{2.15}$	0.93	104
Maize	I	$R_1 = 0.34 + 0.95\,\mathrm{ED}_1^{2.49}$	0.94	39
		$R_2 = -0.19 - 1.44\,\mathrm{ED}_2 + 2.23\,\mathrm{ED}_2^{2.00}$	0.93	9
	II	$R = 0.12\,\mathrm{ED}^{3.70}$	0.93	155

[a] In Season I for maize, subscripts indicate uppermost (1) and subapical (2) ear. A model common to both ears was fitted in Season II. SD: stem diameter; HD: head diameter; BN: branch number; ED: ear diameter. All models were significant at $p < 0.0001$.

[b] Number of individuals sampled.

where α is the initial slope, x_0 the threshold for $y = 0$, and β the degree of curvilinearity at high PGR_C. Reproductive partitioning (P_R) during the critical period was calculated as the ratio between independent estimates of $RepGR_C$ and PGR_C. The ratio between SNP and $RepGR_C$ was used to analyse efficiency in seed set (Ef). Data were grouped by PGR_C intervals to calculate coefficient of variation for reproductive partitioning and efficiency of seed set. Two approaches were used to estimate the minimum assimilate requirement per seed (λ; mg/seed/day). First, we estimated λ as the inverse of the slope of the linear relationship between SNP and $RepGR_C$ in soybean and as the inverse of the maximum efficiency in seed set predicted for sunflower and maize. Second, we determined λ as the average $RepGR_C$ SNP^{-1} for the interval $RepGR_C$ at maximum efficiency ±10%.

3. Results

3.1. Biomass partitioning to reproductive structures

Contrasting availability of resources per plant together with the use of individuals, rather than averages, contributed to the wide range of both $RepGR_C$ and PGR_C (Fig. 1). Plant growth rates (g/day) varied between 0.01 and 4 in soybean, 0.3 and 18 in sunflower, and 0.4 and 12 in maize. Reproductive growth rates (g/day) varied between 0 and 2 in soybean, 0 and 9 in sunflower, and 0 and 5 in maize.

Hyperbolic models adequately described the relationship between $RepGR_C$ and PGR_C in all three species (Table 3). The plant growth threshold for reproductive growth was close to 0 g/day in soybean, intermediate in sunflower and highest in maize (x_0 in Table 3). Soybean and sunflower showed slightly curvilinear responses of $RepGR_C$ to PGR_C (Table 3). In maize, the response of reproductive growth was clearly curvilinear when only the uppermost ear was considered as indicated by the high and significant β (Fig. 1; Table 3). Prolificacy, however, accounted for a significant increase in reproductive growth rate at high PGR_C. When considering subapical ears in maize, the relationship between $RepGR_C$ and PGR_C was almost linear (Fig. 1; Table 3). Plant growth threshold for visible development of the subapical ear in maize was around 3–5 g/plant. Analysis of prolificacy and $RepGR_C$ was made in Season I, when a larger number of plants was sampled at low density. In this group, 95% of the individuals developed a visible subapical ear at the end of the critical period (Fig. 1). Forty percent of these plants, however, failed to produce a seed-bearing ear at maturity. Average $RepGR_C$ (g/day) was 4.1 in prolific plants and 3.4 in non-prolific plants. In prolific plants, reproductive growth rate of the uppermost ear was 17% lower than in non-prolific plants (2.4 vs 2.9 g/day) but reproductive growth rate

Table 3
Parameters (±S.E.) of Eq. (2) describing the relationship between $RepGR_C$ and PGR_C for individual plants of soybean, sunflower and maize[a]

Species	Season	α	X_0 (g/day)	β	R^{2b}
Soybean	I	0.59 ± 0.005	0.04 ± 0.005	0.06 ± 0.004	0.99
	II	0.57 ± 0.040	0.01 ± 0.024 n.s.[c]	0.12 ± 0.026	0.94
Sunflower	I	0.55 ± 0.016	0.10 ± 0.064 n.s.	0.01 ± 0.002	0.99
	II	0.62 ± 0.029	$0.26 \pm 0.087^{**}$	-0.01 ± 0.005 n.s.	0.94
Maize (1E)	I	0.64 ± 0.037	0.72 ± 0.084	0.12 ± 0.014	0.89
	II	0.77 ± 0.059	1.11 ± 0.069	0.13 ± 0.029	0.81
Maize (2E)	I	0.56 ± 0.039	0.79 ± 0.121	0.04 ± 0.010	0.90
	II	0.66 ± 0.037	1.19 ± 0.058	0.00 ± 0.012 n.s.	0.91

[a] In maize, models fitted for $RepGR_C$ of the uppermost (1E) and uppermost + subapical (2E) reproductive structures. Regressions and parameters were significant at $p < 0.0001$, except otherwise indicated.

[b] Coefficient of determination.

[c] Not significant.

** Significant at $p < 0.01$.

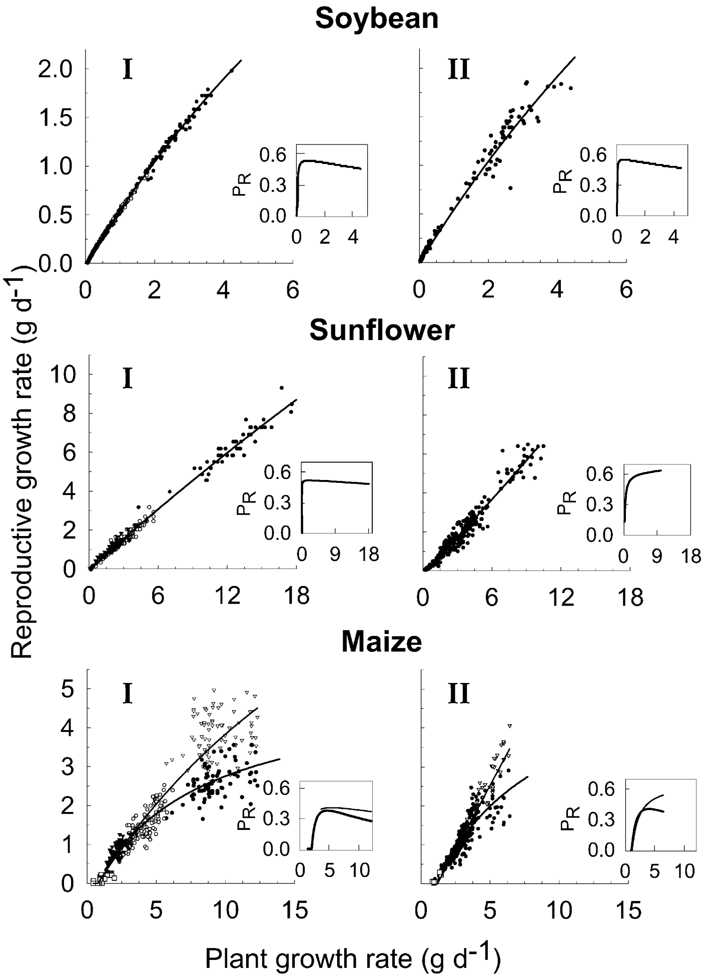

Fig. 1. Reproductive growth rate as a function of plant growth rate during the critical period for seed set in soybean, sunflower and maize individuals during two seasons at Balcarce. In Season I, symbols indicate plant densities. Normal densities (○) were 29.8, 5.8 and 8.5 plants/m^2 in soybean, sunflower and maize, respectively. (●) and (▼) indicate low and high densities, respectively. In maize (□) indicates barren plants and (▽) prolific plants. Insets show the relationship between reproductive partitioning (P_{R}; dimensionless) and $\mathrm{PGR_C}$ according to models in Table 4. In maize, models were fitted for the apical (—) and subapical ears (—).

of the second ear was more than three times greater than in non-prolific plants (1.7 vs 0.5 g/day).

By definition, reproductive partitioning is the proportion of total growth or biomass allocated to reproductive tissues (Donald and Hamblin, 1976; Gifford et al., 1984; Hay, 1995; Sinclair, 1998). These variables, i.e., $\mathrm{RepGR_C}$ and $\mathrm{PGR_C}$, however, are not strictly independent. Lack of independence is accentuated in species with high reproductive allocation. Hence, we also explored the relationship between growth rates of reproductive and vegetative tissues (Fig. 2; Season I). Qualitatively, responses were similar to those observed in Fig. 1. In soybean and sunflower, growth rates of reproductive and vegetative tissues were similar. In maize, $\mathrm{RepGR_C}$ was lower than vegetative growth rate except for few prolific plants. The association between vegetative and reproductive growth was particularly useful to analyse barren plants in maize (open squares in Fig. 2). In this species, two types of barren plants were identified: (i) the ones with no exposed reproductive structures in which $\mathrm{RepGR_C}$ was negligible and assumed to be

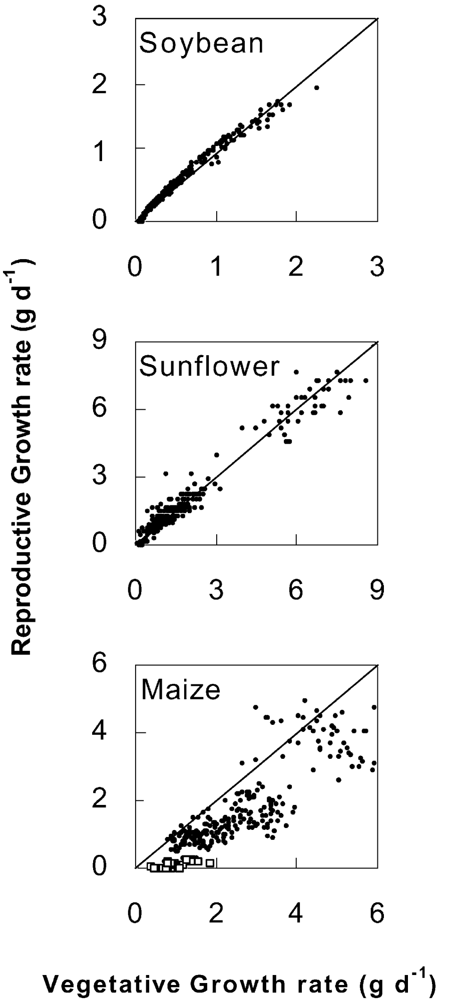

Fig. 2. Relationship between reproductive and vegetative growth rates during the critical period for seed number determination in soybean, sunflower and maize (data from Season I). In maize (□) indicates barren plants. For reference, the line 1:1 is shown.

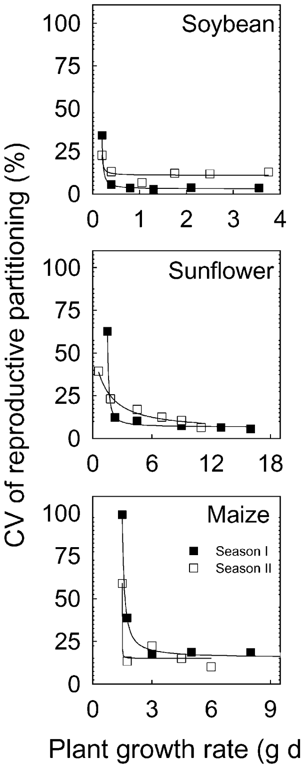

Fig. 3. Coefficient of variation of biomass partitioning to reproductive structures in response to plant growth rate during the critical period for seed number determination in soybean, sunflower and maize grown at Balcarce during two seasons. To analyse CV as a function of PGR$_C$, data were arranged in PGR$_C$ intervals.

0 g/day; (ii) plants with visible reproductive structures which had an average RepGR$_C$ $= 0.15 \pm 0.013$ g/day. Similar results in barren maize plants were found in Season II and in an experiment in which similar high plant densities were arranged in rows 35 cm apart (Vega, 1995, unpublished).

Reproductive partitioning in each species is shown in insets in Fig. 1. For PGR$_C$ greater than 0.02 g/day (soybean) and 0.2 g/day (sunflower), P_R averaged 0.53 in both species. Contrasting, P_R in non-prolific maize plants showed an optimum (0.36–0.46 at PGR$_C$ between 2 and 4 g/day) and declined for PGR$_C$ lower than 2.5 g/day or greater than 4 g/day. When prolificacy was considered, P_R was increased at high PGR$_C$ (inset in Fig. 1). In all three species, reproductive partitioning was lower and highly variable at PGR$_C$ approaching the threshold required to sustain reproductive growth (insets in Figs. 1 and 3). In all three species, significant increase in standard deviation reflected the increase in plant-to-plant variation of reproductive partitioning at PGR$_C$ close to x_0. To allow for the comparison of species, variation was expressed in terms of CV. Maximum CV ranked maize > sunflower > soybean. Variation in reproductive partitioning was particularly important in maize as it sharply increased when PGR$_C$ approached 2 g/day (Figs. 2 and 3).

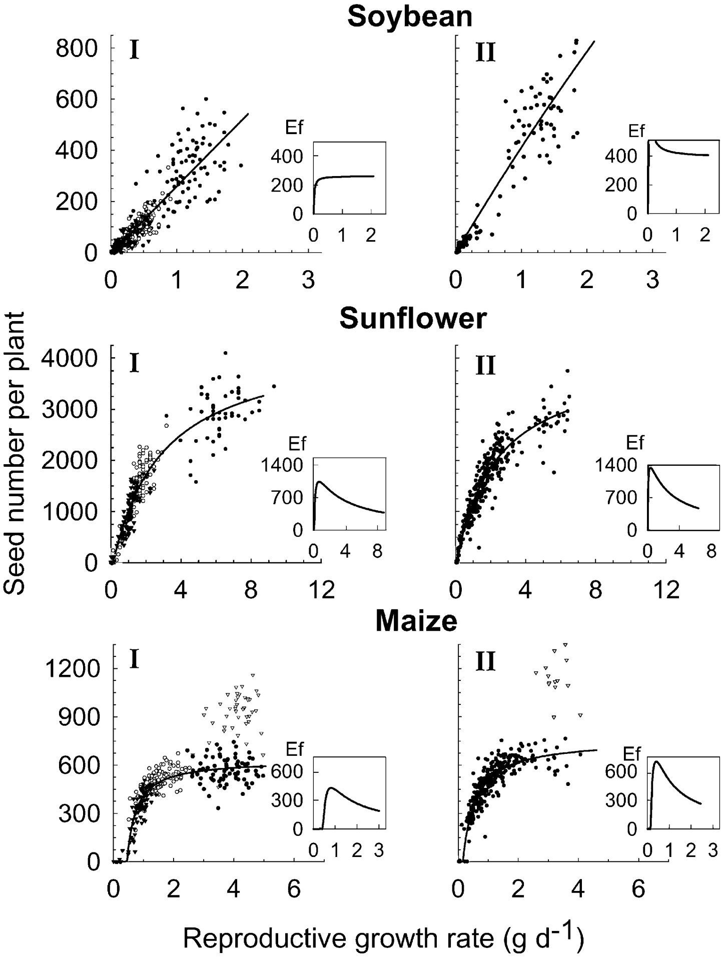

Fig. 4. SNP as a function of $\mathrm{RepGR_C}$ in soybean, sunflower and maize individuals during two seasons at Balcarce. In Season I, symbols indicate plant densities. Normal densities (○) were 29.8, 5.8 and 8.5 plants/m^2 in soybean, sunflower and maize, respectively. (●) and (▼) indicate low and high densities, respectively. In maize (▽) indicates prolific plants. Insets present the predicted efficiency in seed set ($\mathrm{Ef} = \mathrm{SNP\,RepGR_C^{-1}}$; (seeds/g)day) according to models in Tables 5 and 6.

3.2. Reproductive growth and SNP

SNP varied from 0 to 890 in soybean, from 0 to 4096 in sunflower and from 0 to 1348 in maize. The SNP–$\mathrm{RepGR_C}$ relationship was best described by a linear model in soybean and by a hyperbolic function in sunflower and maize (Fig. 4; Tables 4 and 5). In soybean, parameter β — associated with the degree of curvilinearity at high $\mathrm{RepGR_C}$ — was not different from zero hinting at the linearity of the relationship ($p > 0.05$). Seed number showed decreasing responses to $\mathrm{RepGR_C} > 1.5\,\mathrm{g/day}$ in non-prolific maize or $\mathrm{RepGR_C} > 3\,\mathrm{g/day}$ in sunflower. In maize, however, prolificacy alleviated this reproductive limitation in some plants with $\mathrm{RepGR_C} > 2.5\,\mathrm{g/day}$. The threshold of daily reproductive growth required for seed set was negligible in soybean, intermediate in sunflower, and highest in maize (x_0 in Table 4, and a in Table 5).

3.3. Seed number per unit $\mathrm{RepGR_C}$ and minimum $\mathrm{RepGR_C}$ per seed

In all three species, seed set efficiency sharply decreased when $\mathrm{RepGR_C}$ approached the thresholds

Table 4
Parameters (±S.E.) of Eq. (2) fitted to SNP and RepGR$_C$ for individual plants of sunflower and maize[a]

Species	Season	α	X_0 (g/day)	β	R^2[b]
Sunflower	I	1505 ± 79.9	0.12 ± 0.004[**]	0.4 ± 0.03	0.90
	II	1748 ± 92.4	0.05 ± 0.033 n.s.[c]	0.4 ± 0.04	0.88
Maize[d]	I	2104 ± 197.0	0.45 ± 0.022	3.3 ± 0.36	0.87
	II	1782 ± 141.8	0.15 ± 0.020	2.3 ± 0.24	0.79

[a] Regressions and parameters were significant at $p < 0.0001$, except otherwise indicated.
[b] Coefficient of determination.
[c] Not significant.
[d] The fitted model only included seeds in the apical ear of prolific and non-prolific plants.
[**] Significant at $p < 0.01$.

Table 5
Parameters (±S.E.) of the linear model ($y = a + bx$) fitted to SNP and RepGR$_C$ for individual plants of soybean[a]

Season	a	b	R^2
I	−5.1 ± 5.39	263 ± 7.7	0.78
II	2.3 ± 13.88	414 ± 15.9	0.86

[a] Regressions and parameter b were significant at $p < 0.0001$. Parameter a was not significant at $p > 0.05$.

for seed set (insets in Fig. 4). Around these thresholds, hence, Ef varied from lowest (0 seeds RepGR$_C^{-1}$) to maximum. For all three species, standard deviation of SNP RepGR$_C^{-1}$ increased with decreasing PGR$_C$ or RepGR$_C$. Patterns of CV tightly followed those of the standard deviations. Hence, we expressed variation of Ef in terms of CV to allow for the comparison among species (Fig. 5). In sunflower, e.g., CV of Ef was 80% at PGR$_C \cong 0.4$ g/day and 25% at PGR$_C \cong 3$ g/day. For RepGR$_C$ above the thresholds, seed set efficiency was fairly constant in soybean and showed a clear maximum in sunflower and in non-prolific maize (insets in Fig. 4; Tables 4 and 5).

In sunflower, the highest efficiency estimated with the model presented in Table 4 was 1200 (seeds/g)day at RepGR$_C \cong 0.5$ g/day (average for two seasons). In maize, the highest predicted efficiency ((seeds/g)day) was close to 430 at RepGR$_C \cong 0.8$ g/day (Season I) and 700 at RepGR$_C \cong 0.4$ g/day (Season II). In soybean, average efficiency in seed set was 263 (seeds/g)day (Season I) and 414 (seeds/g)day (Season II).

Observed and predicted minimum assimilate requirement per seed (λ) are presented in Table 6.

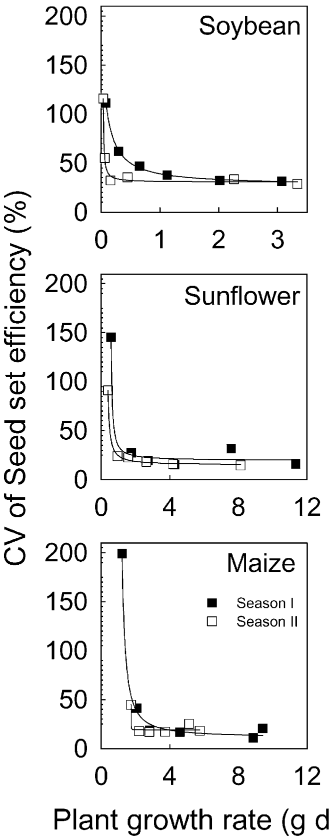

Fig. 5. Coefficient of variation of seed set efficiency in response to PGR$_C$ during the critical period for seed number determination in soybean, sunflower and maize grown at Balcarce during two seasons. To analyse CV as a function of PGR$_C$, data were arranged in PGR$_C$ intervals.

Table 6
Minimum assimilate requirement per seed (λ) calculated as: (i) average $\mathrm{RepGR_C}$ SNP^{-1} (±S.E.) for the interval $\mathrm{RepGR_C}$ at maximum efficiency ±10% ($\mathrm{M_1}$) and (ii) the inverse of maximum seed set efficiency predicted with models in Tables 4 and 5 ($\mathrm{M_2}$)

Species	Season	λ ($\mathrm{M_1}$) (mg/seed/day)	λ ($\mathrm{M_2}$) (mg/seed/day)
Soybean	I	4.2 ± 0.09	3.8
	II	2.9 ± 0.11	2.4
Sunflower	I	1.1 ± 0.05	0.9
	II	0.7 ± 0.08	0.8
Maize	I	2.5 ± 0.08	2.3
	II	1.4 ± 0.07	1.4

In this paper, comparison of λ among species was not performed because of differences in biomass partitioning within the reproductive structure. At the end of the critical period for seed set, biomass accumulation in seeds is normally larger in soybean than in maize and sunflower. In soybean, growth of seeds comprised ≅65% of $\mathrm{RepGR_C}$ at the end of the critical period for seed set. When estimated at the beginning of seed stage in soybean (seed 3 mm long), λ was ≅1.6 mg/day (from $\mathrm{SNP} = 31(\pm 15.6) + 631(\pm 29.2)$-$\mathrm{RepGR_C}$; $R^2 = 0.80$; Season II).

4. Discussion

Reproductive strategies differ among species and influence the relationship between SNP and $\mathrm{PGR_C}$ during the critical period for seed set (Vega et al., 2001). Plant growth thresholds for seed set and non-linearity of the SNP–$\mathrm{PGR_C}$ relationship in sunflower and maize suggest factors other than $\mathrm{PGR_C}$ determine seed number. The model of Charles-Edwards (1984), later thoroughly discussed by Egli (1998), provided an useful framework to investigate two additional processes underlying determination of seed number (i) biomass partitioning to reproductive structures, and (ii) the minimum assimilate requirement per seed.

4.1. Biomass partitioning to reproductive structures

In all three species, hyperbolic models adequately described the relationship between reproductive and shoot growth. At low $\mathrm{PGR_C}$, reproductive partitioning became highly variable and sharply decreased leading to $\mathrm{PGR_C}$ thresholds for reproductive growth (Tables 4 and 5). At high $\mathrm{PGR_C}$, reproductive partitioning was stable or declined slightly in response to increases in $\mathrm{PGR_C}$ (Fig. 1). Among species and despite similarities in the general pattern, non-prolific maize had the largest and soybean the smallest plant growth threshold for reproductive growth and degree of non-linearity (Fig. 1; Tables 4 and 5). Another important difference among species was plant-to-plant variation in reproductive partitioning, which was also largest in maize and smallest in soybean (Figs. 2 and 3).

Reproductive partitioning comprised about half of total plant growth in soybean and sunflower and was generally below 50% in maize (Fig. 2). In soybean, P_R decreased slightly with increase in $\mathrm{PGR_C}$ probably because of an increase in the proportion of late developing pods with lower biomass partitioning to seed (data not shown). In general, however, reproductive partitioning in both soybean and sunflower was fairly stable in response to $\mathrm{PGR_C}$, with the fall in reproductive partitioning only observed in few, very small plants. This agrees with previous studies in soybean (Egli et al., 1985). In sunflower, P_R was found to increase with decreasing resources per plant (Villalobos et al., 1994; Vega, 1996, unpublished). In this work, however, analysis of individuals — within size hierarchies that normally develop within a crop — rather than of the average plant allowed for the detection of an opposite P_R response at $\mathrm{PGR_C}$ close to the threshold for reproductive growth. Interestingly, plants with low reproductive partitioning had the highest height-to-biomass ratio despite being the shortest (data not shown). Promotion of stem elongation in these individuals was possibly related to an altered light environment (Ballaré et al., 1992) and is in agreement with the theory of optimal partitioning to maximise the capture of light, the most limiting factor in our experiments (McConnaughay and Coleman, 1999).

In maize, P_R became highly unstable at $\mathrm{PGR_C} \leq 2\,\mathrm{g/day}$ (Figs. 2 and 3). In this species, moreover, reproductive growth of non-seed bearing plants seemed uncoupled to $\mathrm{PGR_C}$ (Figs. 1 and 2). Importantly, the critical period analysed in this work is probably too long and confounded effects cannot be ignored. For instance, in seed-bearing plants, $\mathrm{RepGR_C}$ included growth after pollination. In contrast, in non-seed bearing plants, failure or inability of sinks to use assimilate efficiently may have at length reduced the overall growth of the reproductive structure (Evans, 1993; Schussler and Westgate, 1994). Additionally, lack of seed may not have affected $\mathrm{PGR_C}$ after pollination leading to plants with relatively high vegetative growth rates. Feedback inhibition of photosynthesis associated with lack of seed is first detected 30–40 days after silking because stems can act as alternative sinks for assimilates (Dalla Valle, 1998; Sadras et al., 2000). Hence, reproductive partitioning in barren maize plants — lower than 0.2 — may be a reflection, rather than being the cause of barrenness at low $\mathrm{PGR_C}$. Importantly, these results highlight the higher sensitivity of reproductive growth at low $\mathrm{PGR_C}$ of maize in comparison with the other two species. Such sensitivity has been frequently associated with loss of priority for assimilates of the ear in relation to other simultaneous sinks (Eastin, 1970; Edmeades et al., 1979; Daynard and Muldoon, 1983; Uhart and Andrade, 1995).

Seed number was tightly associated with reproductive allocation in all three species. This association, however, was linear only in soybean (Fig. 4). Hyperbolic SNP–$\mathrm{RepGR_C}$ relationships in maize and sunflower indicated that: (i) at high $\mathrm{RepGR_C}$, seed number was limited by floret load within the reproductive structure; (ii) reproductive tissues other than seed (sunflower heads and maize cobs and husks) were able to accumulate assimilate (Palmer et al., 1973; Connor and Hall, 1997). In maize, prolificacy contributed to greater reproductive plasticity and efficiency in SNP $\mathrm{RepGR_C^{-1}}$. The expression of prolificacy, however, seemed to depend on a balanced biomass partitioning to both ears, probably as reflection of their synchronism in development and pollination (Prior and Russell, 1975; Cárcova et al., 2000). In contrast, an SNP plateau was not evident in indeterminate soybean.

The relationship between seed number and plant growth rate has been proposed as a means to predict seed number in simulation models (Tollenaar et al., 1992; Andrade et al., 1999; Ritchie and Wei, 2000; Vega et al., 2001). The present work showed that the use of reproductive growth rate as an independent variable improved seed number estimation. This was particularly true in maize, where the variation in SNP observed at $\mathrm{PGR_C}$ close to the threshold for seed set (Vega et al., 2001) was substantially reduced. Ruiz and Dedominici (2000) also improved SNP estimation using $\mathrm{RepGR_C}$ instead of $\mathrm{PGR_C}$ in sunflower.

4.2. Minimum assimilate requirement per seed and efficiency in seed set

Inclusion of λ in Charles-Edwards' model suggests that features of the sink also determine seed number (Egli, 1998 and references therein). Quantification of λ is particularly difficult, however. Indirect estimates of λ proved to be useful in understanding seed number determination in different soybean genotypes (Egli and Zhen-wen, 1991; Ball et al., 2000). To our knowledge, estimates of λ have not been reported for sunflower and maize. Hence, even though roughly, we explored λ in these species on the basis of $\mathrm{RepGR_C}$. Since, by definition, λ is the minimum assimilate requirement per seed, this parameter should only be evaluated under the situation of the highest efficiency in seed set, especially in species where the relationship between SNP and $\mathrm{RepGR_C}$ is non-linear. The agreement between two estimates of λ reinforces the reliability of this parameter (Table 6). Comparison of λ among species should be made with care taking into account differences in seed growth stage. In this work, as we explored the period known to be most critical for seed set, the ranking of λ does not necessarily reflect differences among species as, e.g., in maize and sunflower, seeds were just beginning the filling period. When we used for comparison λ determined at the beginning of seed stage in soybean, species ranked sunflower $<$ soybean $<$ maize.

Efficiency in seed set in terms of seed number produced per unit of growth invested in reproductive tissues was fairly stable for a wide range of $\mathrm{RepGR_C}$ in soybean (inset in Fig. 4) and had a clear optimum in sunflower and maize. In all three species, plant-to-plant variation in Ef at low $\mathrm{PGR_C}$ (Fig. 5) leaded to a low average efficiency in seed set. This effect was more accentuated in maize, particularly in Season I when high barrenness was observed at $\mathrm{PGR_C} < 2\,\mathrm{g/day}$.

Egli and Zhen-wen (1991) and Ball et al. (2000) showed that seed number in soybean is well predicted by the model of Charles-Edwards (1984). In sunflower and maize, however, SNP would be overestimated at low and high $\mathrm{PGR_C}$ because the model neither considers RepGR_C thresholds for seed set nor restrictions in floret morphogenesis. Importantly, the model assumes sinks develop in isolation of each other, in a sequence involving initiation, fertilisation and setting. This assumption seems sound for soybean, a plant with a long critical period for seed set when metameric units develop as more or less independent sinks in terms of position and time. In contrast, in species such as sunflower and maize, flowers develop as cohorts during relatively short periods (Sadras et al., 1985; Bassetti and Westgate, 1994; Cantagallo, 1999). Initiating seeds in these species, hence, should be considered as a community of simultaneously growing and interacting sinks. If the combined demand for assimilate of these multiple sinks is close to or higher than RepGR_C, seed abortion can lead to complete barrenness. This phenomena — hypothesised in the pioneering work by Edmeades and Daynard (1979a,b) — seemed to control SNP, particularly in maize, a species remarkably susceptible to low availability of resources and prone to barrenness (Edmeades and Daynard, 1979b; Tollenaar et al., 1992; Vega et al., 2001).

Interestingly — and even though genotype × environment interactions cannot be excluded — a larger number of individuals with $0 < \text{SNP} < 200$ was observed in maize plants in Season I. These seed-bearing individuals showed the lowest Ef — an indication that RepGR_C exceeded SNP set — suggesting that other processes were down-regulating SNP concomitantly. This phenomena, which can be interpreted as a breakdown of symmetry of identical sinks within the ear, would reflect the outcome of hierarchies and interference among sinks (Ganeshaiah and Uma Shaanker, 1992) probably driven by collateral, e.g., hormonal processes (Stephenson, 1981; Lafitte and Edmeades, 1995; Jones and Setter, 2000; Cárcova and Otegui, 2001). We hypothesise, hence, that λ determines the RepGR_C threshold — reflection of the multiple assimilate requirement of the first developing cohort of flowers — and that it is also positively associated with interference among simultaneously developing sinks. If so, not only seed number, but importantly also stability in seed set efficiency at low PGR_C would be greater in genotypes with low λ. Even though speculative, this conclusion is in agreement with the theory of the self-organising process by Ganeshaiah and Uma Shaanker (1992) which involves simple rules regulating the flow of resource into ovules. Within a species, genotypes differ in λ, probably in an inverse relationship with the number of florets or seed growth rate as found in soybean (Egli, 1998; Ball et al., 2000). In maize and sunflower, no reports on λ exist. Some evidence, however, indicates that intraspecific variation in λ exists, as inferred from the work of several authors (Tollenaar et al., 1992; Lafitte and Edmeades, 1995; Echarte et al., 1998; Luque, 2000).

Finally, predicting seed number is a major weakness of current crop models (Ritchie and Wei, 2000). Inclusion of parameters related to stability in reproductive partitioning at low PGR_C and λ might improve estimation of seed number.

5. Conclusion

Reproductive partitioning during the critical period for seed set was highest in sunflower and soybean ($\cong$50%) and lowest in non-prolific maize. Among species, stability of P_R correlated inversely with a PGR_C threshold for reproductive growth and directly with reproductive plasticity at high PGR_C. Seed number as a function of reproductive growth was adequately described through linear (soybean) and hyperbolic models with *x*-intercepts (sunflower and maize). The Charles-Edwards' model would work in soybean as previously reported (Egli and Zhen-wen, 1991; Ball et al., 2000), but only for a narrow range of PGR_C in sunflower and maize because it neither considers morphogenetic restrictions nor thresholds for seed set. Efficiency in seed set — in terms of SNP $\text{RepGR}_\text{C}^{-1}$ (Ef) — was stable only in soybean. In sunflower and maize, Ef increased with decreasing reproductive growth rate and became highly variable and unstable when RepGR_C was close to the threshold for seed set. The RepGR_C threshold for seed set was highest in maize, possibly as a consequence of a higher minimum combined demand for assimilate, resulting from a higher λ and number of simultaneously developing sinks. Seed number in sunflower, hence, seemed to be limited by floret load at high PGR_C and seed set efficiency rather than by reproductive partitioning. In maize, seed number was related to both reproductive partitioning and seed set efficiency. In this species, sharp decreases in seed set at low PGR_C were associated both with a severe reduction and instability of biomass partitioning to reproductive structures and decreases in Ef. Inclusion of parameters assessing stability in reproductive partitioning at low PGR_C and λ may improve SNP estimation.

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