RESEARCH ARTICLE

Resource distribution and the trade-off between seed number and seed weight: a comparison across crop species

B.L. Gambín[1,2] & L. Borrás[2]

1 Departamento de Producción Vegetal, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, Capital Federal, Argentina
2 Departamento de Producción Vegetal, Facultad de Ciencias Agrarias, Universidad Nacional de Rosario, S2125ZAA Zavalla, Santa Fe, Argentina

Abstract

In grain crops, total sink capacity is usually analysed in terms of two components, seed number and individual seed weight. Seed number and potential individual seed weight are established at a similar timing, around the flowering period, and seed weight at maturity is highly correlated with the potential established earlier. It is known that, within a species, available resources during the seed set period are distributed between both yield components, resulting in a trade-off between seed number and seed weight. Here we tested if this concept could apply for interspecific comparisons, where combinations of numbers and size across species could be related to the total available resources being either allocated to more seed or larger potential individual seed weight during the seed set period. Based on this, species differences in seed weight should be related to resource availability per seed around the period when seed number is determined. Resource availability per seed was estimated as the rate of increase in aboveground biomass per seed around the period of seed set. Data from 15 crop species differing in plant growth, seed number, seed weight and seed composition were analysed from available literature. Because species differed in seed composition, seed weight was analysed following an energy requirement approach. There was an interspecific trade-off relationship between seed number per unit of land area and seed weight ($r = 0.92$; $F(1,13) = 32.9$; $n = 15$; $P < 0.001$). Seed weight of different species was positively correlated ($r = 0.90$; $F(1,13) = 52.9$; $n = 15$; $P < 0.001$) with resource availability per seed around the seed set period. This correlation included contrasting species like quinoa (*Chenopodium quinoa*; $\sim$100 000 seeds m^{-2}, $\sim$4 mg equivalent-glucose seed^{-1}) or peanut (*Arachis hypogaea*; $\sim$800 seeds m^{-2}, $\sim$1000 mg equivalent-glucose seed^{-1}). Seed number and individual seed weight combinations across species were related and could be explained considering resource availability when plants are adjusting their seed number to the growth environment and seeds are establishing their storage capacity. Available resources around the seed set period are proportionally allocated to produce either many small seeds or few larger seeds depending on the particular species.

Introduction

Crop yield is usually analysed as a function of the number of harvested seeds per unit land area and the individual seed weight, with variations in crop yield within a species more related to variations in seed number than in seed weight. For any species, the number of established seeds is highly sensitive to the availability of resources during a particular phase of the crop cycle, with availability frequently estimated as plant or canopy growth rate during the period (Fischer, 1985; Andrade *et al.*, 1999; Vega *et al.*, 2001, Sadras, 2007). This critical period for

yield establishment differs with species but is usually centred on flowering in most crops.

Differences in seed weight at maturity of species are more related to differences in the rate of seed growth during the phase of rapid seed filling than to differences in the duration of seed filling (Egli *et al.*, 1981; Egli, 1998, 2006; Sadras & Egli, 2008). This rate is, in turn, strongly related to the potential seed storage capacity established during the early phase of seed development (Brocklehurst, 1977; Egli *et al.*, 1981; Reddy & Daynard, 1983). The crop developmental phase when this potential individual seed weight is established is known to overlap with the seed determination period to different degrees depending on the particular species (Ney *et al.*, 1993; Calderini *et al.*, 2001; Gambín *et al.*, 2006; Lindström *et al.*, 2006; Yang *et al.*, 2009). This means that the two components representing the total sink capacity, seed number and potential individual seed weight, are established at a similar time.

Smith & Fretwell (1974) developed a theoretical model for understanding the relationships between seed number, seed weight and available resources. Because plant species show a greater variation in seed number than in seed weight (Harper *et al.*, 1970), they proposed that seed number is driven by the available resources and specific seed weight. Thus, understanding the trade-off between seed number and weight in plants can be simplified with a model in which a fixed amount of available resources can be distributed into different combinations of numbers and weight (Smith & Fretwell, 1974):

Seed number = Available resources/Seed weight (1)

This model has been useful to support the stabilising selection theory for seed weight, which establishes that there is an optimum seed weight that maximises parental fitness (Smith & Freztwell, 1974; Sadras, 2007). Later developments highlighted that plant-to-plant variations in available resources because of the genotype or the environment can result in negative, neutral or positive relationships between seed number and weight of individual plants (Venable, 1992).

Because interspecific relationships between seed number and weight are usually negative (Venable, 1992; Turnbull *et al.*, 1999), and species variations in seed weight are mostly related to variations in the rate of seed growth during rapid seed filling (Egli, 1981), it can be hypothesised that species differences in resource distribution to produce seeds or potential seed weight explains the trade-off relationships among both yield components. Current knowledge on phloem unloading

and transport events from sources (leaves) to sinks (seeds) indicates that changes in assimilate production at the source directly affect assimilate availability to developing sinks by changing the pressure difference that governs photoassimilate movement (Patrick, 1997). Hence, differences in plant growth per seed (measured as aboveground plant biomass increase per seed) during the seed set period imply differences in the amount of assimilates available for developing seeds (Gambín *et al.*, 2006, 2008), when the potential storage capacity is being established (Ney *et al.*, 1993; Calderini *et al.*, 2001; Yang *et al.*, 2009). This provides a basis for inter- and intraspecific studies in resource distribution between more or larger seed (number versus weight).

In the present article, we tested the hypothesis that each species allocates resources available during the seed set period proportionally to more seed or larger individual potential seed weight. Based on this, species differences in seed weight should be related to resource availability per seed around the period when seed number is determined, when the potential seed weight is also being established. It is during this period when the trade-off between number and weight is resolved. Resource availability per seed was estimated as canopy aboveground biomass growth rate per established seed around the seed set period. For this, we did a literature review comparing 15 crop species that varied in canopy growth, seed number and individual seed weight. Because species differed in seed composition, seed dry weight was standardised and analysed as mg of equivalent-glucose per seed.

Materials and methods

We searched the Scopus database for titles, abstract or keywords containing the terms 'yield', 'seed number', 'grain number', 'seed weight' or 'grain weight' and 'biomass' or 'crop growth' for different crop species. Table 1 describes, for 15 species, the published articles considered in the analysis. For a particular species, found articles reporting data of seed number, seed weight and crop biomass growth around the seed determination period were included. In order to explore the expected variability for each trait, studies from different environments (which provided variation in light, temperature, soils, etc.) and involving different treatments (e.g. genotypes, years, sowing dates) were incorporated. This was limited, however, by the number of articles found for most species. Within each article, only data from control treatments were used. We were interested in testing how crop species distribute their resources between the two yield components (seed number and individual seed weight) under potential growing conditions at specific environments. For this

Table 1 Details of the articles from the 15 analysed crop species, showing the number of total data points per species (n), considered treatments, country where experiments were conducted, considered seed determination period when available resources were estimated, duration of the seed determination period and corresponding references

Species	N	Treatment (No. of Variants)	Country	Considered Period[a]	Duration (days)	Reference
Barley (Hordeum vulgare)	7	Sowing date (3)	Australia	A − 40 d to A	40	Boonchoo et al. (1998)
		Genotype (4)	Argentina	H − 40 d to H − 10 d or H − 30 d to H	30	Arisnabarreta and Miralles (2008)
Cowpea (Vigna sinensis)	1	Genotype (2)[b]	USA	End vegetative period to EF	28	Turk et al. (1980), Turk and Hall (1980)
Fava bean (Vicia faba)	3	Genotype (3)	Australia	ca. BF to Podding	20–30	Mwanamwenge et al. (1998)
Lentil (Lens culinaris)	3	Genotype (3)	Nepal	A to Podding	20–35	Shrestha et al. (2005)
Maize (Zea mays)	58	Genotype (4)	USA	A − 15 d to A + 15 d	30	Gardner et al. (1990)
		Year (3), sowing date (2)	Argentina	A − 15 d to A + 15 d	30	Cirilo and Andrade (1994, 1996)
		Year (3)	Argentina	A − 15 d to A + 15 d	30	Uhart and Andrade (1995a,b)
		Genotype (12), sites (2)	Argentina	A − 15 d to A + 15 d	30	Gambín et al. (2006)
		Genotype (3), plant density (3), row width (2)	Argentina	A − 15 d to A + 15 d	30	Maddonni et al. (2006)
		Genotype (3)	Argentina	A − 15 d to A + 15 d	30	Gambín et al. (2008)
Pea (Pisum sativum)	10	Genotype (2), plant density (2)	Spain	ca. BF to FSSA	20	Martín et al. (1994)
		Genotype (6)	Australia	ca. BF to FSSA	30	Armstrong and Pate (1994a,b)
Peanut (Arachis hypogaea)	10	Genotype (2), year (3), sowing date (2/1)[c]	Argentina	R3 to R6.5	30–40	Haro et al. (2007)
Quinoa (Chenopodium quinoa)	16	Genotype (4), plant density (2), year (2)	Argentina	BF to EF	20	Bertero and Ruiz (2008)
Rape (Brassica napus)	8	Sites (2), sowing date (3/2)[d]	Australia	BF to EF	30	Hocking and Stapper (2001)
		Fertilisation type (3), year (4)[b]	Poland	F to EF	15	Barłóg and Grzebisz (2004)
Rice (Oryza sativa)	49	Year (2), sites (2), genotype (3/5)[e],	China	PI to A	30	Ying et al. (1998)
		Year (2), genotype (6/8)[f]	Japan	H − 15 d to H + 15 d	30	Takai et al. (2006)
		Genotype (3), year (2)	China	H − 30 d to H	30	Bouman et al. (2006)
		Genotype (2), year (2), sowing date (2)	Taiwan	PI to H	20–30	Jeng et al. (2006)
		Layout irrigation type (5)	Australia	PI to A	35	Beecher et al. (2006)
Sorghum (Sorghum bicolor)	15	Genotype (9), year (2)[b]	Australia	ca.A − 20 d to ca.A + 7 d	27	Borrell et al. (2000)
		Genotype (3)	Argentina	A − 20 d to A + 10 d	30	Gambín et al. (2008)
		Genotype (3)	Australia	ca.A − 20 d to ca. + 7 d	27	van Oosterom et al. (unpublished data)
Soybean (Glycine max)	12	Year (2)[b]	USA	R1 to R5	20	Board and Harville (1993)
		Year (2)[b]	USA	R1 to R5	20	Jiang and Egli (1995)
		Year (2)	USA	R1 to R5	–	Board et al. (1995)

Table 1 continued

Species	N	Treatment (No. of Variants)	Country	Considered Period[a]	Duration (days)	Reference
Sunflower (*Helianthus annuus*)	1	Plant density (3), year (2)[b]	USA	R3 to R6	20	Carpenter & Board (1997a,b)
		Year (2)	USA	R1 to R5	20	Board & Harville (1998)
		Plant density (3), year (2)[b]	USA	R1 to R5	30	Board (2000)
		Genotype (1)	Argentina	A − 20 d to A + 20 d	40	Cantagallo & Hall (2002)
Triticale (*X Triticosecale*)	5	Year (2)	Argentina	ET to A + 7 d	–	Cantarero et al. (1998)
		Genotype (3)	Argentina	Jointing to A	30	Estrada-Campuzano et al. (2008), Estrada-Campuzano et al. (unpublished data)
Wheat (*Triticum aestivum*)	35	Sowing date (4), genotype (2)	Australia	A − 28 d to A + 7 d	35	Bremmer & Davidson (1978)
		Genotypes (15)	Australia	ca. jointing to A	40–50	Regan et al. (1992)
		Year (2), previous crop (2)[g]	Argentina	A − 20 d to A + 7 d	27	Abbate et al. (1997)
		Year (2), genotype (4/5)[h]	Argentina	A − 20 d to A + 7 d	27	Abbate et al. (1998)

[a]Letters represent: PI, panicle initiation; TS, terminal spikelet; H, heading; A, anthesis; BF or R1, beginning of flowering; F, flowering; EF, end of flowering; R3, beginning of podding stage; R3.5, middle of podding stage; R5, beginning of seed filling; R6, maximum seed size.

[b]The article reported averaged data for the source of variation.

[c]Two sowing dates were performed during the first and second year, and one during the third year.

[d]Three sowing dates were performed at one site, and two at the other site.

[e]Three and five genotypes were evaluated the first and second year, respectively.

[f]Six and eight genotypes were evaluated the first and second year, respectively.

[g]Previous crop differed only during 1 year.

[h]Four and five genotypes evaluated the first and second year, respectively.

reason, data involving manipulative treatments aiming to modify seed number or individual seed weight were excluded from the analysis. In addition, data obtained under stressful conditions (e.g. water or nutritional stress) during specific crop developmental stages were excluded.

The period determining seed number for each species is shown in Table 1, and averaged approximately 30 days for most species. This period was considered from approximately anthesis -20 days to anthesis $+10$ days for wheat (Fischer, 1975), 15 days bracketing of anthesis for maize (Early et al., 1967; Andrade et al., 1999), from approximately anthesis -20 days to anthesis for sorghum (Pepper & Prine, 1972), from growth stages R3 to R5.5–R6 for soybean (Jiang & Egli, 1993), from anthesis -30 days to anthesis $+20$ days for sunflower (Cantagallo et al., 1997), from approximately anthesis -30 days to anthesis for triticale (Estrada-Campuzano et al., 2008), from approximately anthesis -30 days to anthesis for barley (Arisnabarreta & Miralles, 2008), from the beginning of flowering to the final stage of seed abortion for pea (Poggio et al., 2005), from approximately anthesis -15 days to anthesis $+15$ days for rice (Takai et al., 2006), from R3 to R6.5 for peanut (Haro et al., 2007) and from beginning to end of flowering for quinoa (Bertero & Ruiz, 2008). Finally, for fava bean and lentil, we assumed the period to be similar to soybean, that is from the beginning of flowering to the pod stage for faba bean, and from anthesis to the pod stage for lentil (Table 1). For rape, the period was assumed to be that of flowering. For cowpea, available articles (Turk & Hall, 1980; Turk et al., 1980) suggested seed number determination period could be calculated from the end of the vegetative stage until the end of flowering (Table 1).

When crop growth rate around the seed set period was not directly available, it was calculated using the reported plant biomass data at the different developmental stages and the number of days between samples. Seed number per unit area was calculated as the quotient between final yield per unit area and individual seed weight in the cases where seed number was not directly reported. All data available on a plant basis were transformed to an area basis using the reported stand density. Resource availability per seed during the seed set period was calculated as the quotient between the crop growth rate around this period and the established seed number per unit land area (mg/day seed^{-1}).

Total number of data points obtained from each individual article depended on the particular treatment combinations (see Table 1). For example, an article having three genotypes in one growing season meant a total of three data points (e.g. lentil; Table 1), or another article having four genotypes growing at two

stand densities during two experimental years gave a total of 16 data points (e.g. quinoa; Table 1). However, inconsistencies between the number of data points and treatments can be found for cowpea, maize, rape, sorghum and soybean. This is because we detailed all considered treatments (e.g. number of genotypes, years, sowing dates, planting densities) independently of any further data averaging performed by authors. For example, for cowpea, Turk & Hall (1980) and Turk et al. (1980) analysed seed number and seed weight for two genotypes, but they reported averaged data for total crop dry matter. For this reason, there was only one data point for this species. Further detailed information for each species is indicated in Table 1.

Because species differ in seed composition, seed dry weight was assessed using an energy requirement approach (mg equivalent-glucose seed^{-1}). This was carried out following the estimates used by Sinclair & de Wit (1975). Knowing the relative composition of seeds and conversion coefficients (one unit of glucose can produce 0.83 units of carbohydrates, 0.40 units of proteins or 0.33 units of lipids), they tabulated a conversion coefficient for the production of the whole seed from glucose for each species. Based on comparable seed composition, triticale was assumed to have a similar energy requirement to wheat, and quinoa was assumed to have a similar energy requirement to oat (Avena sativa) (Nájera, 1992; Tohver et al., 2005).

Linear and nonlinear models were fitted to the parameters under study, using the iterative optimisation technique of Table Curve V 3.0 (Jandel Scientific, 1991). We used an allometric nonlinear model to describe the relationship between seed number and final seed weight. To assess the strength of linear relationships, Pearson's correlation coefficient (r) was calculated and tested for significance using an F-test.

Results

The species analysed showed large variations in both harvested seed number and individual seed weight. Seed number varied from 844 ± 58 (peanut) to $104\,157 \pm 11\,849$ (quinoa) harvested seeds m^{-2}, and seed weight from 3.4 ± 0.1 (quinoa) to 1065 ± 48 (peanut) mg equivalent-glucose seed^{-1} (2.4 ± 0.1 and 458 ± 21 mg dry weight seed^{-1} for quinoa and peanut, respectively). Both yield components varied by three orders of magnitude across crop species.

There was a significant nonlinear negative correlation ($r = 0.92$; $F(1,13) = 32.9$; $n = 15$; $P < 0.001$) between seed number and seed weight when all species were considered, showing that the species producing the smallest individual seeds at maturity were those with
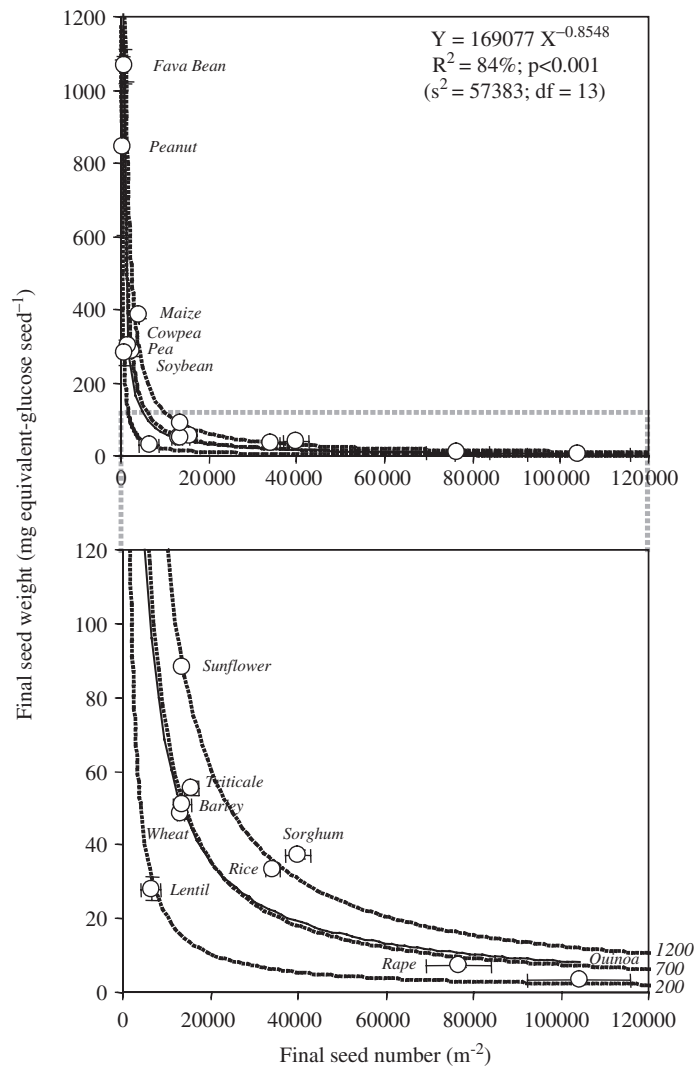
Figure 1 Relationship between individual seed weight (in glucose requirements) and harvested seed number per unit land area for 15 crop species. Each symbol represents the species average of all available data (see Table 1 for details on each species). Dotted curves show three different seed number and weight combinations for similar harvest yields (200, 700 and 1200 g equivalent-glucose m^{-2}). The solid curve shows the nonlinear model fitted to the data. Bars indicate the SE of the mean.

the most seeds (Fig. 1). This general relationship was clear when contrasting species were analysed, but the association between seed number and weight was not always negative when specific species are considered (e.g. maize had a greater number of seeds of larger weight than soybean; and lentil had fewer seeds of smaller weight than wheat). The adjusted curvilinear relationship between number and weight was close to the 700 g equivalent-glucose m^{-2} yield curve, but the range covered the yield curve of 200 (fava bean, pea and lentil) and 1200 g equivalent-glucose m^{-2} (maize, sunflower, sorghum and rice) (Fig. 1). Final yield

(g equivalent-glucose m^{-2}) showed no association with either of the two yield components.

Crop growth rate during the period of seed set varied from 2.9 ± 0.5 (lentil) to 31.9 ± 1.2 (maize) g m^{-2} day^{-1}. Interspecific variations in seed number showed no clear relationship with the crop growth rate during the period (Fig. 2a). The same result was apparent for seed weight; there was no correlation between the crop growth rate around the seed set period and the seed weight when all species were analysed together (Fig. 2b). However, there was a significant, positive linear relationship between
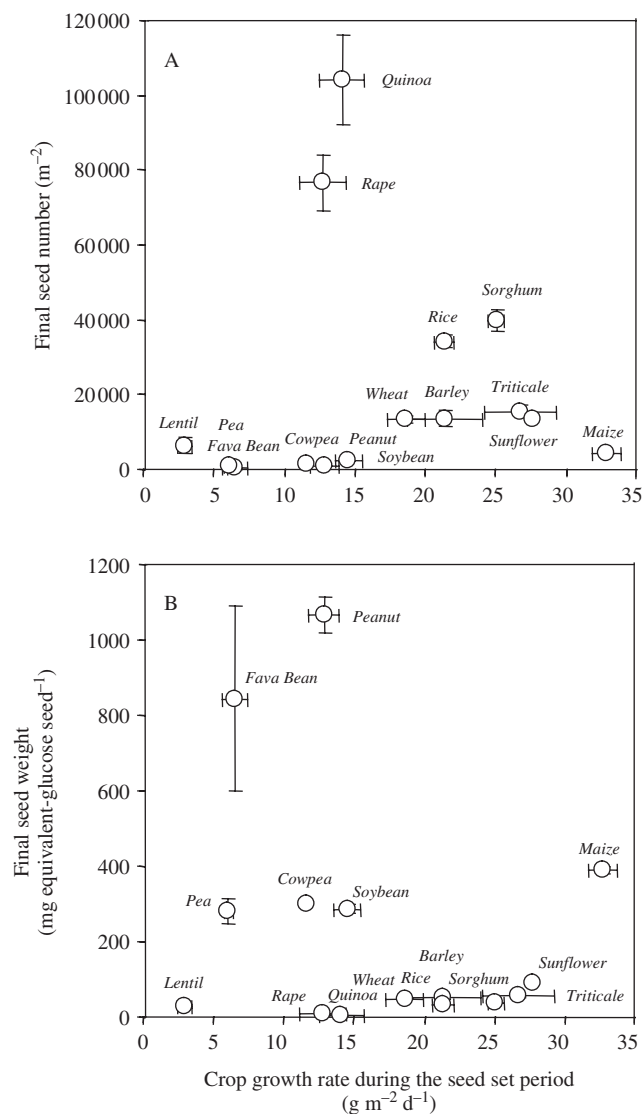
Figure 2 Relationship between the crop growth rate around the seed number determination period and (a) the number of harvested seeds per unit land area and (b) the individual seed weight (in glucose requirements). Each symbol represents the species average of all available data (see Table 1 for details on each species). Bars indicate the SE of the mean.

the crop yield (g equivalent-glucose m^{-2}) and the crop growth rate around the period when seed number was determined ($r = 0.88$; $F(1,13) = 46.1$; $n = 15$; $P < 0.01$), where the species with the greatest crop growth rates (maize and sorghum) were the species with the largest yields. This correlation was also significant when crop yield (g m^{-2}) was analysed on a dry weight basis and uncorrected for seed energy requirements ($r = 0.90$; $F(1,13) = 52.9$; $n = 15$; $P < 0.01$).

We hypothesised that each species allocates resources available during the seed set period proportionally to more seed or larger individual potential seed weight.

Based on this, interspecific variations in seed weight could be predicted by differences in the availability of resources per established seed during the period of seed set, when the trade-off between seed number and weight is resolved. There was a significant correlation ($r = 0.90$; $F(1,13) = 52.9$; $n = 15$; $P < 0.001$) between the crop growth rate per seed around the period of seed set and the final seed weight (Fig. 3). This relationship was highly significant even when seed weight was uncorrected by energy requirements ($r = 0.97$; $F(1,13) = 196$; $n = 15$; $P < 0.001$), or when the two biggest seeds (fava bean and peanut) were excluded from the analysis ($r = 0.96$;
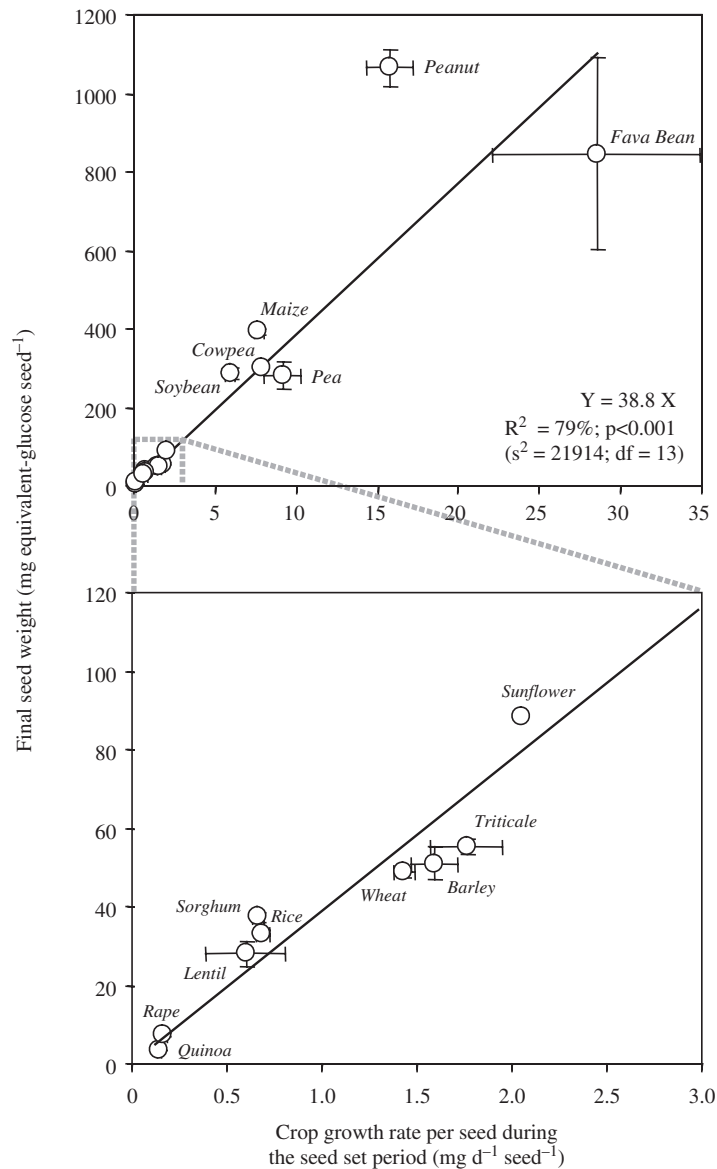
Figure 3 Relationship between the crop growth rate per seed during the seed number determination period and the individual seed weight (in glucose requirements). The crop growth rate per seed was calculated as the quotient between the rate of aboveground biomass gain per day during the period of seed number determination and the harvested seed number per unit land area. Each symbol represents the species average of all available data (see Table 1 for details on each species). The solid line shows the linear model fitted to the data. Bars indicate the SE of the mean.

$F(1,11) = 127$; $n = 13$; $P < 0.001$). The species showing the smallest seeds at maturity and the largest number of seeds were also the ones with the slowest crop growth rates per individual seed during seed establishment, and the species with the largest seeds and the fewest seeds were those with the highest resources per seed during the period when seed number was determined. Also, species showing a higher crop growth rate per seed during this period because of differences in crop growth rate and not in seed number (e.g. maize

versus lentil) were correlated with higher seed weights as well.

Discussion

Available resources during the seed set period are either allocated to produce many small seeds or few larger seeds depending on the particular species. A trade-off between seed number and weight was clear when contrasting species were compared, but was less evident

when specific species were analysed (e.g. maize versus soybean; lentil versus wheat; Fig. 1). Differences in seed weight across species could be easily analysed in terms of resources available per established seed during the seed set period, when the potential seed weight is also being established (Fig. 3). As hypothesised, the trade-off between seed number and weight was resolved around this crop developmental stage.

We have demonstrated that the Smith & Fretwell (1974) model applies for comparing how crop species establish their yield components when this analysis is carried out during the period when seed number is determined. This interspecific analysis adds to and supports recent considerations of Sadras (2007) when applying the same model for studying intraspecific seed number and weight trade-off relationships in crop species. The tight dependence of both seed number and weight to the available resources around a specific period during crop development has important productive implications. As species allocate available resources into one yield component or the other, improved plant growth during the seed number determination period is needed to enhance total sink capacity either by a higher seed number or a higher seed weight.

The Smith & Fretwell (1974) model establishes that seed number adjusts in response to genetic variation in seed weight. In their framework, seed weight is more genetically controlled and less plastic than seed number in response to changes in availability of resources during the period when both yield components are being established. Previous studies have shown seed weight to be highly heritable, much more than seed number (see Sadras, 2007, and references therein). Here we have shown how to document the intrinsic genetic variation in seed weight across species using models describing the determination of seed number (Smith & Fretwell, 1974; Sadras, 2007).

Recent evidence supports the concept that seed weight plays an important role in modulating seed numbers (Sadras, 2007; Sadras & Egli, 2008). In this context, the implication behind the interspecific relationship shown in Fig. 3 needs further study. It was not demonstrated whether seed number responds to changes in plant growth because of a pre-established seed weight (as hypothesised by Sadras, 2007) or if potential seed weight is dependent upon the resource distribution among developing florets from early in development. It is expected, however, that both mechanisms are active to some degree; each specific genotype has a pre-established lower and upper limit for potential seed weight that are genetically determined, and the particular potential set in any given environment depends on the available resources per established seed during the seed set period. In both cases, this means an assimilate anticipation for grain filling, which might contribute to the optimum balance between offspring number and weight enhancing parental fitness.

The presented simple approach could be used for understanding and predicting other inter- and intraspecific relationships between these yield components because of the genotype or the environment. When the approach was proposed for understanding intraspecific relationships between seed number and weight in maize (Gambín et al., 2006, 2008) a similar pattern was evident: the relationship between plant growth rate around the seed set period and seed number helped explain changes in seed weight. This indicates that the same concepts could be applied for analysing intraspecific relationships in any crop species.

In summary, interspecific relationships between yield components (seed number and final seed weight) can be analysed considering available resources when plants are adjusting their seed number to the growth environment and seeds are establishing their storage capacity. Analysed species showed a similar efficiency in allocating resources into one or the other yield component. Total resources available around the seed set period are proportionally allocated to produce either many small seeds or few larger individual seeds depending on the particular species.

Acknowledgements

References

Abbate P.E., Andrade F.H., Culot J.P., Bindraban P.S. (1997) Grain yield in wheat: effects of radiation during spike growth period. *Field Crops Research*, **54**, 245–257.

Abbate P.E., Andrade F.H., Lázaro L., Bariffi J.H., Berardocco H.G., Inza V.H., Marturano F. (1998) Grain yield increase in recent Argentine wheat cultivars. *Crop Science*, **38**, 1203–1209.

Andrade F.H., Vega C., Uhart S., Cirilo A., Cantarero M., Valentinuz O. (1999) Kernel number determination in maize. *Crop Science*, **39**, 453–459.

Armstrong E.L., Pate J.S. (1994a) The field pea crop in S.W. Australia. I. Patterns of growth, biomass production and photosynthetic performance in genotypes of contrasting morphology. *Australian Journal of Agricultural Research*, **45**, 1347–1362.

Armstrong E.L., Pate J.S. (1994b) The field pea crop in S.W. Australia. II. Effects of contrasting morphology and

environment on reproductive performance. *Australian Journal of Agricultural Research*, **45**, 1363–1378.

Arisnabarreta S., Miralles D.J. (2008) Critical period for grain number establishment of near isogenic lines of two- and six-rowed barley. *Field Crops Research*, **107**, 196–202.

Barlóg P., Grzebisz W. (2004) Effect of timing and nitrogen fertilizer application on winter oilseed rape (*Brassica napus* L.). I. Growth dynamics and seed yield. *Journal of Agronomy and Crop Science*, **190**, 305–313.

Beecher H.G., Dunn B.W., Thompson J.A., Humphreys E., Mathews S.K., Timsina J. (2006) Effect of raised beds, irrigation and nitrogen management on growth, water use and yield of rice in south-eastern Australia. *Australian Journal of Experimental Agriculture*, **46**, 1363–1372.

Bertero H.D., Ruiz R.A. (2008) Determination of seed number in sea level quinoa (*Chenopodium quinoa* Willd.) cultivars. *European Journal of Agronomy*, **8**, 186–194.

Board J.E., Harville B.G. (1993) Soybean yield component responses to a light interception gradient during the reproductive period. *Crop Science*, **33**, 772–777.

Board J.E., Wier A.T., Boethel D.J. (1995) Source strength influence on soybean yield formation during early and late reproductive development. *Crop Science*, **35**, 1104–1110.

Board J.E., Harville B.G. (1998) Late-planted soybean yield response to reproductive source/sink stress. *Crop Science*, **38**, 763–771.

Board J. (2000) Light interception efficiency and light quality affect yield compensation of soybean at low plant populations. *Crop Science*, **40**, 1285–1294.

Boonchoo S., Fukai S., Hetherington S.E. (1998) Barley yield and grain protein concentration as affected by assimilate and nitrogen availability. *Australian Journal of Agricultural Research*, **49**, 695–706.

Borrell A.K., Hammer G.L., Henzell R.G. (2000) Does maintaining green leaf area in sorghum improve yield under drought? II. Dry matter production and yield. *Crop Science*, **40**, 1037–1048.

Bouman B.A.M., Yang X., Wang H., Wang Z., Zhao J., Chen B. (2006) Performance of aerobic rice varieties under irrigated conditions in North China. *Field Crops Research*, **97**, 53–65.

Bremmer P.M., Davidson J.L. (1978) A study of grain number in two contrasting wheat cultivars. *Australian Journal of Agricultural Research*, **28**, 431–441.

Brocklehurst P.A. (1977) Factors controlling grain weight in wheat. *Nature*, **66**, 348–349.

Cantagallo J.E., Chimenti C.A., Hall A.J. (1997) Number of seeds per unit area in sunflower correlates well with a photothermal quotient. *Crop Science*, **37**, 1780–1786.

Cantagallo J.E., Hall A.J. (2002) Seed number in sunflower as affected by light stress during the floret differentiation interval. *Field Crops Research*, **74**, 173–181.

Cantarero M.G., Badiali O.J.J. (1998) Modificación de la cantidad de radiación en pre y pos antesis en triticale:

Rendimiento en grano y componentes. Actas del IV Congreso Nacional de Trigo. Mar del Plata, Argentina.

Calderini D.F., Savin R., Abeledo L.G., Reynolds M.P., Slafer G.A. (2001) The importance of the period immediately preceding anthesis for grain weight determination in wheat. *Euphytica*, **119**, 199–204.

Carpenter A.C., Board J.E. (1997a) Branch yield components controlling soybean yield stability across plant populations. *Crop Science*, **37**, 885–891.

Carpenter A.C., Board J.E. (1997b) Growth dynamics factors controlling soybean yield stability across plant populations. *Crop Science*, **37**, 1520–1526.

Cirilo A.G., Andrade F.H. (1994) Sowing date and maize productivity. II. Kernel number determination. *Crop Science*, **34**, 1044–1046.

Cirilo A.G., Andrade F.H. (1996) Sowing date and kernel weight in maize. *Crop Science*, **36**, 325–331.

Early E.B., McIlrath W.O., Seif R.D. (1967) Effects of shade applied at different stages of plant development on corn (*Zea mays* L.) production. *Crop Science*, **7**, 151–156.

Egli D.B. (1981) Species differences in seed growth characteristics. *Field Crops Research*, **4**, 1–12.

Egli D.B. (1998) *Seed Biology and the Yield of Grain Crops*. Wallingford, UK: CAB International.

Egli D.B. (2006) The role of the seed in the determination of yield of grain crops. *Australian Journal of Agricultural Research*, **57**, 1237–1247.

Egli D.B., Fraser J., Leggett J.E., Poneleit C.G. (1981) Control of seed growth in soya beans (*Glycine max* (L.) Merrill). *Annals of Botany*, **48**, 171–176.

Estrada-Campuzano G., Miralles D.J., Slafer G.A. (2008) Yield determination in triticale as affected by radiation in different development phases. *European Journal of Agronomy*, **28**, 597–605.

Fischer R.A. (1975) Yield potential in dwarf spring wheat and the effect of shading. *Crop Science*, **15**, 607–613.

Fischer R.A. (1985) Number of kernels in wheat crops and the influence of solar radiation and temperature. *Journal of Agricultural Science*, **105**, 447–461.

Gambín B.L., Borrás L., Otegui M.E. (2006) Source–Sink relations and kernel weight differences in maize temperate hybrids. *Field Crops Research*, **95**, 316–326.

Gambín B.L., Borrás L., Otegui M.E. (2008) Kernel weight dependence upon plant growth at different grain-filling stages in maize and sorghum. *Australian Journal of Agricultural Research*, **59**, 280–290.

Gardner F.P., Valle R., McCloud D.E. (1990) Yield characteristics of ancient races of maize compared to a modern hybrid. *Agronomy Journal*, **82**, 864–868.

Haro R.J., Otegui M.E., Collino D.J., Dardanelli J.L. (2007) Environmental effects on seed yield determination of irrigated peanut crops: links with radiation use efficiency and crop growth rate. *Field Crops Research*, **103**, 217–228.

Harper J.L., Lovell P.H., Moore K.G. (1970) The shapes and size of seeds. *Annual Review of Ecology and Systematics*, **1**, 327–356.

Hocking P.J., Stapper M. (2001) Effects of sowing time and nitrogen fertiliser on canola and wheat, and nitrogen fertiliser on Indian mustard. I. Dry matter production, grain yield, and yield components. *Australian Journal of Agricultural Research*, **52**, 623–634.

Jandel Scientific. 1991. *Table Curve V. 3.0, User's manual, Version 3.0, AISN software*. Corte Madera, CA: Jandel Scientific.

Jiang H., Egli D.B. (1993) Shade induced changes in flower and pod number and flower and fuit abscission in soybean. *Agronomy Journal*, **85**, 221–225.

Jiang H., Egli D.B. (1995) Soybean seed number and crop growth rate during flowering. *Agronomy Journal*, **87**, 264–267.

Jeng T.L., Tseng T.H., Wang C.S., Chen C.L., Sung J.M. (2006) Yield and grain uniformity in contrasting rice genotypes suitable for different growth environments. *Field Crops Research*, **99**, 59–66.

Lindström L.I., Pellegrini C.N., Aguirrezábal L.A.N., Hernández L.F. (2006) Growth and development of sunflower fruits under shade during pre and early post-anthesis period. *Field Crops Research*, **96**, 151–159.

Maddonni G.A., Cirilo A.G., Otegui M.E. (2006) Row width and maize grain yield. *Agronomy Journal*, **98**, 1532–1543.

Martín I., Tenorio J.L., Ayerbe L. (1994) Yield, growth, and water use of conventional and semileafless peas in semiarid environments. *Crop Science*, **34**, 1576–1583.

Mwanamwenge J., Loss S.P., Siddique K.H.M., Cocks P.S. (1998) Growth, seed yield and water use of faba bean (*Vicia faba* L.) in a short-season Mediterranean-type environment. *Australian Journal of Experimental Agriculture*, **38**, 171–180.

Nájera J.R. (1992) Development of an infant food from quinoa (*Chenopodium quinoa* Willd). Technological aspects and nutritional consequences. PhD Thesis, University of Lund, Sweden.

Ney B., Duthion C., Fontaine E. (1993) Timing of reproductive abortions in relation to cell division, water content, and growth of pea seeds. *Crop Science*, **33**, 267–270.

Patrick J.W. (1997) Phloem unloading: sieve element unloading and post-sieve element transport. *Annual Review of Plant Physiology and Plant Molecular Biology*, **48**, 191–222.

Pepper G.E., Prine G.M. (1972) Low light intensity effects on grain sorghum at different stages of growth. *Crop Science*, **12**, 590–593.

Poggio S.L., Satorre E.H., Dethiou S., Gonzalo G.M. (2005) Pod and seed numbers as a function of photothermal quotient during the seed set period of field pea (*Pisum sativum*) crops. *European Journal of Agronomy*, **22**, 55–69.

Reddy V.M., Daynard T.B. (1983) Endosperm characteristics associated with rate of grain filling and kernel size in corn. *Maydica*, **28**, 339–355.

Regan K.L., Siddique K.H.M., Turner N.C., Whan B.R. (1992) Potential for increasing early vigour and total biomass in spring wheat. II. Characteristics associated with early vigour. *Australian Journal of Agricultural Research*, **43**, 541–553.

Sadras V.O. (2007) Evolutionary aspects of the trade-off between seed size and number in crops. *Field Crops Research*, **100**, 125–138.

Sadras V.O., Egli D.B. (2008) Seed size variation in grain crops: allometric relationships between rate and duration of seed growth. *Crop Science*, **48**, 408–416.

Shrestha R., Siddique K.H.M., Turner N.C., Turner D.W., Berger J.D. (2005) Growth and seed yield of lentil (*Lens culinaris* Medikus) genotypes of West Asian and South Asian origin and crossbreds between the two under rainfed conditions in Nepal. *Australian Journal of Agricultural Research*, **56**, 971–981.

Sinclair T.R., de Wit C.T. (1975) Photosynthate and nitrogen requirements for seed production by various crops. *Science*, **189**, 565–567.

Smith C.C., Fretwell S.D. (1974) The optimal balance between size and number of offspring. *The American Naturalist*, **108**, 499–506.

Takai T., Matsuura S., Nishio T., Ohsumi A., Shiraiwa T., Horie T. (2006) Rice yield potential is close related to crop growth rate during late reproductive period. *Field Crops Research*, **96**, 328–335.

Tohver M., Kann A., Täht R., Mihhalevski A., Hakman J. (2005) Quality of triticale cultivars suitable for growing and bread-making in northern conditions. *Food Chemistry*, **89**, 125–132.

Turk K.J., Hall A.E. (1980) Drought adaptation in cowpea. II. Influence of drought on plant growth and relations with seed yield. *Agronomy Journal*, **72**, 428–433.

Turk K.J., Hall A.E., Asbell C.W. (1980) Drought adaptation in cowpea. I. Influence of drought on seed yield. *Agronomy Journal*, **72**, 413–420.

Turnbull L.A., Rees M., Crawley M.J. (1999) Seed mass and competition/colonization trade-off: a sowing experiment. *Journal of Ecology*, **87**, 899–912.

Venable D.L. (1992) Size-number trade-offs and the variations of seed size with plant resource status. *The American Naturalist*, **140**, 287–304.

Vega C.R.C., Andrade F.H., Sadras V.O., Uhart S.A., Valentinuz O.R. (2001) Seed number as a function of growth. A comparative study in soybean, sunflower, and maize. *Crop Science*, **41**, 870–878.

Uhart S.A., Andrade F.H. (1995*a*) Nitrogen deficiency in maize: I. Effects on crop growth, development, dry matter partitioning, and kernel set. *Crop Science*, **35**, 1376–1383.

Uhart S.A., Andrade F.H. (1995*b*) Nitrogen deficiency in maize: II. Carbon-nitrogen interaction effects on kernel number and grain yield. *Crop Science*, **35**, 1384–1389.

Yang Z., van Oosterom E.J., Jordan D.R., Hammer G.L. (2009) Pre-anthesis ovary development determines genotypic differences in potential kernel weight in sorghum. *Journal of Experimental Botany*, **60**, 1399–1408.

Ying J., Peng S., He Q., Yang H., Yang C., Visperas R.M., Cassman K.G. (1998) Comparison of high-yield rice in tropical and subtropical environments. I. Determinants of grain and dry matter yields. *Field Crops Research*, **57**, 71–84.