Seed dry weight response to source–sink manipulations in wheat, maize and soybean: a quantitative reappraisal

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Abstract

Determining to what degree seed weight differences are due to competition among seeds for insufficient source is critical for the rational design of breeding and management strategies aimed at maximizing crop yields. While the crop physiology literature cites many examples of source and/or sink yield limitations during seed filling, interpretation of these data has usually been qualitative in nature, biasing our view of the source–sink yield limitations during this period. In the present review, we applied a quantitative approach for determining the magnitude of seed dry weight changes in response to manipulations in assimilate availability during seed filling for previously published articles in wheat (\textit{Triticum aestivum}) maize (\textit{Zea mays} \textit{L.}) and soybean (\textit{Glycine max} \textit{L.}). This quantitative approach demonstrates that yield is usually more sink than source limited during seed filling in the three crops, though: (i) interspecific variation exists in the magnitude of limitation, and (ii) intraspecific variability is larger in soybean than in cereals. Seeds of wheat appeared to grow mostly at saturated assimilate availability, so yield is mainly sink limited in all growing conditions\texttimes cultivar combinations explored in the analysis. Soybeans seem to experience a large degree of co-limitation by the source and the sink, as seeds greatly respond to source–sink modifications. Maize displayed a consistent trend to dramatic reductions in seed dry weight when assimilates produced during seed filling are reduced, but a virtual lack of responsiveness to improvements in potential availability of assimilates per growing seed. This results in a sink-limited crop in most growing conditions, but a source-limited crop if resource availability is strongly reduced during seed filling.

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1. Introduction

Improved understanding of yield responses to alterations in assimilate availability during different

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phenological phases has been a major advance in crop physiology. It has provided clear evidence that crops experience periods during the growing cycle when yield is mainly limited by the source strength, the sink capacity, or co-limited by both. From these experiments the so-called “critical periods”, when crop yield is strongly source-limited, have been reasonably well established for most major crops. As crop yield is more strongly related to seed number per unit land area than to mean seed dry weight, it has not been surprising that critical periods for yield determination
have been identified to be around the crop phenological phase when final seed number is determined (Early et al., 1967; Fischer, 1975, 1985; Egli, 1998).

In spite of the fact that seed number per unit land area is the most important yield component, seed dry weight is also an important contributor to seed yield. Illustrating this, Fig. 1 shows the relationship between maize seed yield and seed number per unit area in tropical (Chapman and Edmeades, 1999) and temperate environments (Otegui, 1995). Although overall it is clear that the number of seeds per unit area is the dominant component in yield determination, it is also evident that for any given seed number there is a wide range in achievable yield due to variations in mean seed dry weight. Results depicted in Fig. 1 are for maize, but similar relationships can be drawn from reported results of studies conducted with other crops (Brooks et al., 1982; Wardlaw and Wrigley, 1994; Blum, 1998; Egli, 1998; Frederick and Bauer, 1999).

When designing strategies aimed to maximize yield by plant breeding or crop management, it is important to know the extent to which differences in seed dry weight are a result of competition among seeds within one plant. Therefore, many articles have reported yield responses of major crops to source–sink manipulations during the seed filling period. However, in most cases, the interpretation of results has been strongly qualitative in nature. That is, whenever seed weight changed in response to a manipulation altering the source–sink ratio, and the magnitude of this seed dry weight change was statistically significant, the common conclusion has been that seed filling was source limited. On the other hand, if changes in seed dry weight were not significant it would be concluded that seed growth and seed yield were sink-limited during seed filling (i.e., that the assimilate availability from actual photosynthesis during seed filling plus reserve remobilization exceeded the demand from the growing seeds). Although the conclusion of a sink-limited yield based on no seed dry weight response may be correct, a statistically significant change in seed dry weight may not always be indicative of a source limitation if that change is not biologically relevant. From a quantitative perspective, if a rather large manipulation of the source–sink ratio during seed filling only results in slight responses in seed dry weight, it should not be concluded that the non-manipulated control was source-limited; i.e., although the seed dry weight response might be statistically significant it might be biologically and agronomically insignificant.

A more quantitative approach may clarify at least some of the conflicting results from individual studies. For instance, the disagreement among studies on the importance of the source or sink limitation to crop yield during the seed filling period is magnified when
crop species are compared. At present, few reports have been published comparing seed weight responsiveness to source–sink manipulations during the seed filling period between different crops (e.g., a comparison among summer crops was reported by Andrade and Ferreiro, 1996), although speculations on this matter have been made (Egli and Bruening, 2001).

In the present study, we compared the magnitude of the seed weight response with the magnitude of the alteration in assimilate availability during the seed filling period in order to test quantitatively whether source or sink limitations in seed growth have been predominant in wheat, maize and soybean. For this purpose, the literature on the subject was extensively reviewed and data from various sources were reanalyzed with single response curves for each species following the approach used by Slafer and Savin (1994) for wheat. Further, these responses were compared, and we propose and discuss alternative hypotheses for the differences observed among species.

2. Seed dry weight response to alterations in assimilate availability during grain filling

2.1. Database and analysis

To study quantitatively the response of seed dry weight to the availability of assimilates needed during the seed filling period we used the method proposed by, and detailed in, Slafer and Savin (1994). Briefly, treatment data of each study were compared to the corresponding non-manipulated control, both for assimilate availability per growing seed produced during seed filling as well as for seed dry weight. The representation of both variables in relative units allowed for comparisons of all data from very different sources. For example, if a particular crop was experimentally manipulated by removing 50% of the seeds at flowering (and the treatment effectively reduced seed number to 50% of the control), and seed dry weight increased from 100 to 110 mg per seed, this was assumed to be a 100% increase in potential assimilate availability per seed that resulted in a 10% increase in seed dry weight when both variables are compared to the untreated control. When the assimilate availability manipulations were imposed at the middle of the seed filling period, increased assimilate availability was assumed to be proportional to the fraction of the seed filling period affected. That is, if the assimilate availability manipulation in the above given example would have been imposed when 25% of the seed filling period had already elapsed, it was represented as a 75% increase in potential assimilate availability relative to the untreated control. The effective length of assimilate manipulation within the seed filling period was estimated for each individual study comparing the number of days, thermal units or phenological phases that were affected in the manipulated treatment, compared to the control treatment. If the treatment altered the duration of the seed filling period, this was not taken into account. In soybean, R5 was considered the start of the seed filling period and R6 the start of the effective seed filling period (Board et al., 1994; Egli, 1997; Egli and Bruening, 2001). Also, although it has been shown that seed dry weight susceptibility to changes in assimilate availability per seed varies throughout the seed filling period (Calderini et al., 2001), this was not taken into account in our study. Thus, for each crop we plotted the relative seed dry weight response against the relative change in the potential availability of assimilates per seed produced during seed filling of all the revised papers. A brief description of the literature reviewed is given in Table 1. This illustrates the genotypic variability explored in each case, the type of source–sink manipulation treatments imposed, and the country where experiments were conducted.

There are two main assumptions in the methodology described above. The first is that the source provided by organs other than green leaves is negligible in maize and soybean. Thus, when the reduction in assimilate availability per seed was obtained by defoliation in these two crops, potential source reduction was simply expressed as the proportion of leaf area removed from the plants. This simple approach did not apply in the case of wheat, because of the important photosynthetic function of the spikes during post-anthesis. In this crop, therefore, an additional correction was made to data obtained from defoliation experiments, in which we assumed that spikes intercepted 21% of incident solar radiation (Thorne et al., 1988). On the other hand, it is noteworthy that most data used in this work with source reductions during seed filling in wheat were obtained from shading...
rather than from defoliation (30%) experiments (Table 1).

Table 1
Description of the number of tested genotypes, the type of manipulative treatment used to alter assimilate availability per seed during seed filling, and the country where the experiment was conducted

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of genotypes</th>
<th>Type of treatment</th>
<th>Country</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wheat</td>
<td>4</td>
<td>Defoliation, chemical leaf desiccation</td>
<td>Israel</td>
<td>Blum et al. (1983)</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Seed removal</td>
<td>Mexico</td>
<td>Calderini (unpublished)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Shading</td>
<td>Argentina</td>
<td>Caldiz and Sarandón (1988)</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>Shading, seed removal</td>
<td>Mexico</td>
<td>Fischer and HilleRisLambers (1978)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Shading</td>
<td>Mexico</td>
<td>Fischer (1975)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Shading</td>
<td>USA</td>
<td>Grabau et al. (1990)</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Seed removal</td>
<td>Russia</td>
<td>Koshkin and Tararina (1989)</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>Defoliation</td>
<td>Argentina</td>
<td>Kruk et al. (1997)</td>
</tr>
<tr>
<td></td>
<td>58</td>
<td>Seed removal</td>
<td>Belgium, Sweden</td>
<td>Ledent and Stoy (1985)</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>Seed removal</td>
<td>USA</td>
<td>Ma et al. (1990)</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>Seed removal</td>
<td>USA</td>
<td>Ma et al. (1995)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Shading, seed removal</td>
<td>UK</td>
<td>Martinez-Carrasco et al. (1988)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Seed removal</td>
<td>Argentina</td>
<td>Miralles and Slafer (1995)</td>
</tr>
<tr>
<td></td>
<td>82</td>
<td>Chemical leaf desiccation</td>
<td>Australia</td>
<td>Nicolas and Turner (1993)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Shading</td>
<td>Argentina</td>
<td>Savin and Slafer (1991)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Defoliation, seed removal</td>
<td>USA</td>
<td>Simmons et al. (1982)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Seed removal</td>
<td>Argentina</td>
<td>Slafer and Miralles (1992)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Seed removal</td>
<td>Argentina</td>
<td>Slafer and Savin (1994)</td>
</tr>
<tr>
<td>Maize</td>
<td>2</td>
<td>Defoliation</td>
<td>USA</td>
<td>Afuakwa et al. (1984)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Shading, stand reduction</td>
<td>Argentina</td>
<td>Andrade and Ferreiro (1996)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Seed removal</td>
<td>Argentina</td>
<td>Borrás and Otegui (2001)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Seed removal</td>
<td>USA</td>
<td>Borrás et al. (2003)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Seed removal</td>
<td>Argentina</td>
<td>Cirilo and Andrade (1996)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Shading</td>
<td>USA</td>
<td>Early et al. (1967)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Defoliation</td>
<td>USA</td>
<td>Egharevba et al. (1976)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Defoliation, seed removal</td>
<td>USA</td>
<td>Jones and Simmons (1983)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Defoliation, seed removal</td>
<td>USA</td>
<td>Jones and Brenner (1987)</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>Seed removal</td>
<td>USA</td>
<td>Kiniry et al. (1990)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Shading</td>
<td>USA</td>
<td>Reed et al. (1988)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Seed removal</td>
<td>USA</td>
<td>Schoper et al. (1982)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Shading</td>
<td>USA</td>
<td>Tollenaar and Daynard (1978a)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Defoliation</td>
<td>Canada</td>
<td>Tollenaar and Daynard (1978b)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Shading</td>
<td>Argentina</td>
<td>Uhart and Andrade (1995)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Stand reduction</td>
<td>USA</td>
<td>Walker et al. (1988)</td>
</tr>
<tr>
<td>Soybean</td>
<td>1</td>
<td>Shading, stand reduction</td>
<td>Argentina</td>
<td>Andrade and Ferreiro (1996)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Defoliation</td>
<td>USA</td>
<td>Board et al. (1994)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Defoliation, seed removal</td>
<td>USA</td>
<td>Board and Harville (1998)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Shading, seed removal</td>
<td>USA</td>
<td>Egli and Bruening (2001)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Shading, seed removal</td>
<td>USA</td>
<td>Egli et al. (1985)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Shading, defoliation, seed removal</td>
<td>USA</td>
<td>Egli et al. (1989)</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Shading</td>
<td>USA</td>
<td>Egli (1997, 1999)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Defoliation, seed removal</td>
<td>USA</td>
<td>McAlister and Krober (1958)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Defoliation, seed removal</td>
<td>France</td>
<td>Munier-Jolain et al. (1998)</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Seed removal</td>
<td>USA</td>
<td>Specht et al. (1999)</td>
</tr>
</tbody>
</table>

The second assumption was that sink strength has no effect on the non-manipulated source capacity.

Although we are aware of evidence showing re-adjustments in canopy photosynthesis to compensate for artificially imposed alterations in the source–sink ratio during seed filling, this response has always been
quite minor when compared with the magnitude of the source–sink manipulation. In addition, this sort of compensation is also known to be cultivar × environment dependent (Crafts-Brandner and Egli, 1987; Rajcan and Tollenaar, 1999; Kumudini, 2002). Thus, in some cases the increases in assimilate availability per seed due to partial or total sink removal treatments may have been slightly over estimated if this treatment resulted in a reduction in canopy photosynthesis.

For each species, a bilinear with plateau model (Eqs. (1) and (2)) was fitted to the response of relative seed dry weight (Y) to the relative change in potential assimilate availability per seed (X). All genotypes and environments were included in the model

\[ Y = a + bX \quad \text{for} \quad X \leq c, \]

\[ Y = d \quad \text{for} \quad X > c, \]

where \( a \) is the intercept, \( b \) the slope at the response part of the curve, \( c \) the saturation value at which further increases in relative assimilate availability per seed are no longer expected to increase relative seed dry weight, and \( d \) the plateau value that summarizes the maximum seed dry weight as a percentage of the controls. The model was fitted using an iterative optimization technique (Jandel Scientific, 1991). This bilinear model was used as a simplification of the theoretical hyperbolic model (Jenner et al., 1991). It simply predicts that there is a response range where any assimilate availability modification impacts seed dry weight, and that, from a particular threshold upwards, seeds grow in a saturated medium in which seed dry weight no longer changes. Also, we fitted a response curve to the 10% less responsive and 10% most responsive data to describe the extremes found in literature for each species. For this, we sorted all data from each species, disregarding their origin, by changes in assimilate availability per seed, and for each set of 10 continuous values the highest and lowest seed dry weight response points were used. Then, from the total of 250 data points available for wheat the 25 most and the 25 least responsive seed dry weights across the magnitude of the treatments imposed were used. The same procedure was applied to maize and soybean. We fitted the bilinear with plateau model to these two groups of values representing the extreme responses. It is important to note that the most responsive cases are the ones that had the largest seed dry weight increase per unit assimilate availability increase and the largest seed dry weight decrease per unit assimilate availability decrease. Conversely, for the less responsive cases, they were the data points that increased or decreased the least per unit of assimilate availability per seed increase or decrease, respectively.

2.2. Seed dry weight responses

Whenever assimilate availability per seed during seed filling was altered either up or down, wheat seeds showed a high degree of homeostasis in seed dry weight at physiological maturity (Fig. 2). This result agrees with previous findings (Slafer and Savin, 1994) obtained from a more limited wheat data set. Mean seed dry weight of all data within the response part of the curve changed ca. 0.12 relative to the change in potential availability of assimilates per seed produced during seed filling (Table 2). In other words, seed dry weight was only marginally responsive to changes in current photosynthesis during seed filling. This is in agreement with the fact that assimilates stored before seed filling can normally contribute more than 50% of final seed dry weight in stressful conditions in this species (Gent, 1994).

Considering the 10% least responsive data points, wheat crops experienced no source limitations for seed growth, as no change in seed dry weight was found in response to either increases or decreases in assimilate availability per seed (Table 2). Regarding the 10% most responsive cases found in wheat, there was a 25% seed dry weight change per 100% change in assimilate availability per seed during seed filling (Table 2). Thus, although wheat crops can undergo some degree of source limitation in some stressful conditions, even in the worst environments seed dry weight did not change (i.e., decreased or increased) in a proportion similar to the changes imposed on the source. It is clear that cases may be found for wheat in which seed growth varies from being completely sink limited to being co-limited by both source and sink, but not a single case of complete source limitation during seed growth has been reported. Moreover, for the extreme 10% of the cases exhibiting co-limitation, that imposed by the post-anthesis source may account for only ca. 25% of the final weight.
Maize seed dry weight response to changes in assimilate availability per seed after flowering had noticeable differences depending on whether assimilates were decreased or increased (Fig. 3). Our literature review clearly showed that, whenever maize crops were exposed to a reduced source strength, seed dry weight was decreased describing a statistically significant and biologically relevant pattern. The mean slope between changes in seed dry weight and changes in assimilate availability was 0.75 in the response part of the curve (Table 2). Even the 10% least responsive cases found in literature evidenced significant seed dry weight decreases due to limitations in assimilate availability per seed produced during seed filling when assimilates were reduced (Table 2). The 10% most responsive cases found in literature demonstrated that the magnitude of the seed dry weight decrease matched the reduction in assimilate availability, showing several values over the 1:1 ratio of complete source limitation for seed growth (Fig. 3). Then, it can be reliably concluded that maize seed growth is highly source-limited when tested by reducing the amount of assimilates produced during seed filling.

In contrast, whenever assimilate availability per seed was increased during the post-flowering period, maize seed dry weight tended to increase only marginally (Fig. 3). Maximum mean seed dry weight increase averaged only 16%. For the most and least responsive cases this increase was around 25% and virtually 0%, respectively (Table 2). This response of maize seed dry weight to increased assimilate availability (i.e., positive x-axis values) shows that seeds of this species normally grow near the saturation level of assimilate...
availability that maximizes their final weight. As a consequence of the dramatically different seed weight response to reductions and improvements in the post-flowering availability of resources per seed, the saturation level appears to be rather low (<20%; Table 2). Therefore, it seems that in most cases maize seed growth (and crop yield) is co-limited by both the source and the sink. To avoid yield penalties in this crop, it is important to keep an adequate source strength respect to the seed sink set at flowering, while acknowledging that yield improvements may more easily come from sink strength increases near flowering rather than from improvements in the post-anthesis source availability per seed. A corollary is that maize crops should benefit from any agricultural practice that avoids potential losses in post-anthesis photosynthesis of the canopy, while not necessarily benefiting from improvements in this trait.

In soybean, seed dry weight was quite responsive to increased source per seed, but with a rather large degree of variation (Fig. 4). Seed dry weight increased up to 112% in the most responsive cases, while the least responsive cases showed an increase of only 12% (Table 2). Mean seed dry weight response to increased assimilate availability was around 46%. Taking into account this mean value, it seems soybean maximum seed dry weights are rarely achieved because of rather large source limitations for seed growth under normal growing conditions.

When assimilate availability was reduced due to shading or defoliation treatments, soybean seed dry weight decreased. Although the magnitude of the response was not negligible, it was not close to reaching the 1:1 ratio either (Fig. 4), even when the most responsive cases were considered (Table 2). The sub-sample of the 10% least responsive cases exhibited a small seed dry weight reduction in response to decreased assimilate availability (Table 2), which did not differ significantly (P > 0.05) from zero. Note that conclusions based on extreme values from soybean must be drawn with care because of the small number of data points included in the analysis (Table 2).

When the response pattern of the three species is compared, it is evident that there are clear differences among them that are independent of the environment or cultivars used in each particular experiment. While wheat yield is mostly independent of current assimilates produced during the seed filling period, maize yield, and to some degree that of soybean as well, is

### Table 2
Parameters describing mean seed dry weight response of wheat, maize and soybean as well as those of the extreme 10% most responsive (maximum 10%) or less responsive (minimum 10%) data

<table>
<thead>
<tr>
<th>Species</th>
<th>Response curve</th>
<th>Seed weight change per assimilate availability change in the response part of the curve (dimensionless)</th>
<th>Assimilate availability break point (%)</th>
<th>Seed weight response at assimilate availability saturation (%)</th>
<th>Theoretical average seed weight reduction if potential assimilates were reduced 100% (%)</th>
<th>R²; n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wheat</td>
<td>All data</td>
<td>0.117 ± 0.008</td>
<td>109 ± 17</td>
<td>11 cd</td>
<td>13</td>
<td>0.56; 250</td>
</tr>
<tr>
<td></td>
<td>Maximum 10%</td>
<td>0.250 ± 0.027</td>
<td>104 ± 25</td>
<td>25 b</td>
<td>24</td>
<td>0.82; 25</td>
</tr>
<tr>
<td></td>
<td>Minimum 10%</td>
<td>−0.007 ± 0.015</td>
<td>103 ± 488</td>
<td>−5 e</td>
<td>1</td>
<td>0.01; 25</td>
</tr>
<tr>
<td>Maize</td>
<td>All data</td>
<td>0.749 ± 0.063</td>
<td>18 ± 6</td>
<td>16 c</td>
<td>23</td>
<td>0.82; 100</td>
</tr>
<tr>
<td></td>
<td>Maximum 10%</td>
<td>1.120 ± 0.097</td>
<td>18 ± 6</td>
<td>25 b</td>
<td>100</td>
<td>0.97; 10</td>
</tr>
<tr>
<td></td>
<td>Minimum 10%</td>
<td>0.266 ± 0.113</td>
<td>18 ± 26</td>
<td>4 d</td>
<td>27</td>
<td>0.50; 10</td>
</tr>
<tr>
<td>Soybean</td>
<td>All data</td>
<td>0.409 ± 0.060</td>
<td>99 ± 22</td>
<td>46 a</td>
<td>37</td>
<td>0.72; 63</td>
</tr>
<tr>
<td></td>
<td>Maximum 10%</td>
<td>0.666 ± 0.063</td>
<td>169 ± 20</td>
<td>112c</td>
<td>59</td>
<td>0.99; 6</td>
</tr>
<tr>
<td></td>
<td>Minimum 10%</td>
<td>0.279 ± 0.300</td>
<td>17 ± 73</td>
<td>12c</td>
<td>22</td>
<td>0.09; 6</td>
</tr>
</tbody>
</table>

a A bilinear with plateau model was fitted describing a response range where any assimilate availability modification impacts seed dry weight and that, from a particular break-point, seeds grow in a saturated medium that maximizes seed weight. Parameters are shown ±S.E. Mean seed dry weight response at assimilate availability saturation was compared using a student’s t-test, and different letters stand for significant differences (P < 0.05).

b Not statistically different form zero (P < 0.05).

c Insufficient data to compare values statistically.
highly dependent on the amount of assimilates produced during this phase. On the other hand, wheat and maize crops had very similar responses whenever assimilate availability per seed was increased (Figs. 2 and 3). This means that, expected yield increase due to enhanced assimilate availability during seed filling should not be expected in either of these cereals (Table 2). At assimilate availability saturation levels, the mean response of soybean seed dry weight differs markedly from that of wheat and maize. Even the most responsive cases of wheat and maize had a significantly lower seed dry weight increase at enhanced assimilate availability ranges when compared to the mean soybean seed dry weight response at this range ($P < 0.05$; Table 2).

In order to clarify the range of assimilate availability in which seeds from the three species normally grow, we made a simple schematic diagram that summarizes and simplifies the interpretation of results from our quantitative approach (Fig. 5). For this purpose, we used the conceptual framework proposed by Jenner et al. (1991), where the response of storage accumulation to assimilate supply conforms to a hyperbolic pattern. As can be simply extrapolated from our quantitative analysis, wheat seeds grown under normal or more extreme growing conditions are close to the supply level of precursors that maximize seed accumulation rates and final seed dry weight (Richards, 1996; Slafer et al., 1996; Calderini et al., 2001; Araus et al., 2002). The assimilate availability range in which maize seeds grow under most cropping conditions would be close to the saturation level, as indicated by the lack of a clear seed dry weight response to increases in assimilate availability per seed (Fig. 3). But, at the same time, when this crop is subjected to extreme growing conditions, limited
source availability sharply reduces seed biomass accumulation. Thus, the range of assimilate availability maize seeds might explore lies in the most responsive part of the curve in Fig. 5 (Early et al., 1967; Egha-ervba et al., 1976; Jones and Brenner, 1987). Supported by our quantitative analysis (Fig. 4), the assimilate availability range at which soybean seeds are usually growing would be within the response part of the curve (Fig. 5), where any change (i.e., increase or decrease) in the level of assimilates is reflected in final seed dry weight (Egli et al., 1985; Egli, 1998).

3. Proposed hypotheses for crop differences

There are at least three alternative, non-exclusive characteristics of wheat, maize and soybean that may partially explain the remarkably different responses of seed growth to changes in assimilate availability per seed during seed filling. Unfortunately, the literature is fragmented and incomplete, with considerable differences in the amount and accuracy of data available for each crop. This restriction may limit in some cases the robustness and confidence of our analyses. The main differences between these three crops, that drive the differential responses to source–sink manipulations during seed filling are due to: (i) the efficiency with which stem reserves can be remobilized to buffer short-comings in actual photosynthesis per seed during seed growth, (ii) the timing when potential seed weight is actually determined during seed filling, and (iii) the most common radiation levels to which these crops are exposed during the sink size determination period compared with those during the sink-filling period.

3.1. Capacity to utilize stored assimilates during seed filling

In the three crops under study, changes in the source–sink ratio during seed filling are frequently accompanied by changes in stem dry weight (McAlister and Krober, 1958).
1958; Tollenaar, 1977; Savin and Slafer, 1991). Stem reserves can serve as a buffer between the supply of current photoassimilates produced by the source and the demand by the sink(s).

Maize crops are highly inefficient in the use of assimilates stored before flowering for seed growth. Although stored non-structural carbohydrates increase the buffering capacity for seed growth, these are mainly consumed in maintenance processes when severe stress occurs (Kiniry et al., 1992). Maize efficiency in the production of seed biomass from pre-flowering stored assimilates has been estimated to be around 0.26 g of seed g\(^{-1}\) of stored carbohydrates (Kiniry et al., 1992). On the other hand, the efficiency of wheat in remobilizing pre-flowering stored assimilates and using them for seed growth was calculated to be around 0.68–0.78 g of seed g\(^{-1}\) of stored assimilates (Austin et al., 1977; Kiniry, 1993; Gebbing et al., 1999). This 3- to 4-fold higher capacity of wheat vs. maize in the utilization of pre-flowering stored assimilates may be one of the causes of the large difference between them in seed dry weight response to reductions in current assimilate production during seed filling, while wheat seems quite independent of the assimilate flux level determined by current photosynthesis.

As far as we are aware, no estimates of soybean remobilization efficiency from stored non-structural carbohydrates for seed production have been made. Following the methodology used for wheat by Austin et al. (1977), a rough estimation was made for this crop based on data published by Hume and Criswell (1973), in which the distribution and utilization of \(^{14}\)C-labeled assimilates were studied at different phenological stages. Computed values indicated 0.53 and 0.64 g of seed g\(^{-1}\) of assimilates for data from each available growing season. This range of values is intermediate between those of wheat and maize, in agreement with the species differences in seed dry weight sensitivity to reductions in current photosynthesis during seed filling. Thus, it seems to support the hypothesis that the efficiency of remobilization of assimilates stored in stems for seed production may underlie the species differences in seed dry weight sensitivity to reductions in current photosynthesis during seed filling (Fig. 6).

3.2. Plasticity in potential seed dry weight throughout seed filling

Present knowledge of seed development has established that differences in seed size at physiological

![Fig. 5. Schematic diagram showing the hyperbolic relationship describing the dependence of seed storage accumulation on the level of assimilates available (Jenner et al., 1991) together with the expected average limits (plain line) and possible extreme situations (dotted line) that experience wheat, maize and soybean seeds during seed filling.](image)

![Fig. 6. Wheat, maize and soybean seed dry weight sensitivity to reductions in assimilate availability per seed produced during the seed filling period plotted against the mean values reported in the literature of remobilization efficiency for each crop.](image)
maturity are already evidenced at earlier stages of the seed filling period. For instance, the number of cells in the endosperm (cereals) or in the cotyledons (soybean), and the number of starch granules determined before, or just after, the onset of rapid seed growth rate correlate well with seed size at maturity (Brocklehurst, 1977; Egli et al., 1981; Reddy and Daynard, 1983).

The use of seed moisture content as a way to normalize seed development across a wide range of environments has shown value as an estimator of the percent final seed dry weight achieved at any particular moment during seed filling. This measure may also be used to prove that differences in seed dry weight are often achieved throughout the seed filling period in wheat, maize and soybean (Fig. 7; Swank et al., 1987; Calderini et al., 2000; Borras et al., 2003). The use of seed water content as an estimator of final seed volume has recently been shown to be a useful alternative approach for estimating potential seed dry weight. As seed density (seed dry-matter per unit seed volume, g cm\(^{-3}\)) is a rather stable trait (e.g., Millet and Pinthus, 1984), differences in seed dry weight of genotypes of the same species in response to treatments are strongly related to modifications in maximum seed volume. In both cereals (Saini and Westgate, 2000) and in soybean (Swank et al., 1987), maximum seed volume is determined earlier than maximum seed dry weight.

Because maximum seed volume is an estimator of final seed dry weight, its determination throughout the seed filling period may have important implications in understanding seed response capacity to source–sink manipulations. Seeds of crops under analysis exhibit remarkable differences in the timing of maximum water content achievement. Those of wheat and maize reach maximum seed volume quite early in their development, having accumulated by that time only ca. 35% of their final dry weight (Fig. 8). On the other hand, soybean seeds reach their maximum volume much later in relative terms, after having accumulated ca. 80% of their final dry weight (Fig. 8). We hypothesize that the later onset of maximum seed volume (and, therefore, potential final weight) extends the capacity of soybean seeds to modify their weight in response to enhanced source strength. The consequence of this extended capacity is the ability of soybean to increase current seed dry weight whenever assimilate availability is enhanced during this phase. Supporting this hypothesis, it has been shown that enhanced assimilate availability around mid seed filling resulted in increased seed dry weight after a similar increase had been detected in maximum water content.

**Fig. 7.** Percent maximum seed dry weight and moisture decline during seed filling in wheat (open circles, Egli and TeKrony, 1997; closed circles Calderini et al., 2000), maize (open squares, Westgate and Boyer, 1986; open circles, Egli and TeKrony, 1997; closed circles, Borras et al., 2003) and soybean (closed circles, Swank et al., 1987; open circles, Egli and TeKrony, 1997) seeds. Within each species the range specifies the explored seed dry weights actually observed at physiological maturity.
content (Egli et al., 1985; Egli, 1990). Enhanced assimilate availability allowed seed water content to be increased at a higher rate and during a longer period than the control (Egli et al., 1985). As the timing when maximum water content is achieved defines the duration of the seed filling period (Egli, 1990), enhanced assimilate availability may increase the duration of this phase in soybean seeds (Egli et al., 1985, 1989; Egli and Bruening, 2001).

3.3. Environmental conditions before and after the onset of seed growth

Because of the sensitivity of maize to low temperatures, it is often sown relatively late in most temperate growing areas, and these restrictions are even more drastic for soybean. This fact, together with the need of a minimum length of vegetative development to generate a commercially acceptable yield, chronologically delays seed filling of these crops to a period when solar radiation levels are decreasing. On the other hand, the period for seed number determination frequently occurs under solar radiation levels higher than those occurring during seed filling. In other words, in the case of maize and soybean, the potential availability of assimilate is much higher during the period when the sink strength is set than when the filling of these sinks has to take place. The opposite is true for wheat, where radiation levels normally increase throughout the growing season (Fig. 9). These environmental differences have been proposed as a hypothesis explaining crop differences in source strength limitations for the achievement of maximum seed weight (Egli, 1999; Egli and Bruening, 2001).

This environmental hypothesis has the underlying physiological assumption that crops having their seed filling under environmental conditions that are less favorable than those experienced during seed set would have their seeds growing far below the assimilate availability saturation point that maximizes seed dry weight. From this point of view, and supporting the results shown in Fig. 2, winter crops like wheat and barley should be more insensitive to assimilate enhancements than summer crops, as seed growth of the former takes place under a higher radiation input than that experienced at seed set (Fig. 9). Soybean, on the other hand, should be the crop with the highest seed dry weight response to increased assimilate availability per seed during seed filling, as seed growth takes place at lower radiation levels than those...
registered during the period for seed number determination (Fig. 9). Maize establishes seed number and seed dry weight in environmental conditions similar to those experienced for soybean, but differences between these phases are not as drastic as for the oil crop (Fig. 9).

4. Concluding remarks

Key issues emerging from this study are:

1. Seeds of wheat, maize and soybean are usually growing within different assimilate availability ranges, independently of the specific genotype or growing condition (Fig. 5). Because of this, crops differ in their relative source/sink yield limitation during the seed filling period. Growth of wheat seeds is apparently more sink- than source-limited in most conditions. Soybean seeds seem to experience a large degree of co-limitation, with a large degree of variation due to genotypes and environments (Fig. 4). Maize shows a consistent trend towards a dramatic reduction in seed dry weight if the post-anthesis availability of assimilates is reduced, accompanied by a virtual lack of responsiveness to improvements in availability of assimilates per seed.

2. The greater plasticity of soybean seeds for establishing final seed sink potential may be the most important trait behind its higher seed dry weight response to increased assimilate availability during seed filling when compared to wheat and maize (Fig. 8). These differences may be associated with differences among species in their timing of achieving maximum seed volume, as well as with differences in the environmental (radiation and temperature) conditions each crop generally experiences during seed filling.

3. Differences in the efficiency of remobilization of assimilates temporarily stored in the stem for seed production may be an important aspect determining seed dry weight response when assimilate availability is reduced. Wheat, maize and soybean differ markedly in their capacity to utilize assimilates stored before seed filling for seed biomass deposition, and this may be the cause of their divergent seed dry weight sensitivity to a shortage in current assimilate production during this phase (Fig. 6).
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