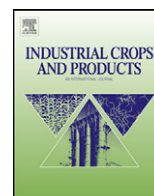




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Seed-yield and yield components response to source–sink ratio in annual and perennial species of *Lesquerella* (Brassicaceae)

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ABSTRACT

Although the annual *Lesquerella fendleri* is the prime candidate for the development of a lesquerolic rich oil-seed crop, within this genus there are other species available to breeders, some of which are perennials. However, the feasibility of a perennial crop of *Lesquerella* is not clear because increases in seed-yield tend to reduce perenniality. The objective of this work was to determine the effect of the source–sink ratio on seed yield and yield components in annual and perennial species of *Lesquerella*. We predicted that (i) due to differences in allocation patterns of annual and perennial species, seed-yield and yield components in perennials would be less affected by the source–sink ratio (higher stability) than in annuals and (ii) since seed-weight has been found to be the most stable yield component in other crops and their wild relatives, most of the variation in seed-yield as a consequence of source–sink ratios would be determined by changes in the number fruits per plant and the number of seeds per fruit. A field experiment was carried out in Chubut, Patagonia Argentina in a complete randomized design with four treatments to examine source–sink relationships in four species of *Lesquerella*, two annuals (*L. angustifolia*, *L. gracilis*) and two perennials (*L. pinetorum*, *L. mendocina*). We used either shading (reduction of source) or removal of flower-buds (reduction of sink) to develop a range of source–sink relationships. All four species showed a similar yield response to source–sink variations. Seed-yield was lower in shaded plants, although the timing of shading influenced this response. Flower-bud removal resulted in a significant increase in seed-yield. Seed-yield differences among source–sink treatments were best explained by changes in the number of fruits per plant than by the number of seeds per fruit. Source–sink manipulations had no effect on seed weight. Flower-bud removal significantly increased the number of fruits per plant in all species except for *L. mendocina*. The number of seeds per fruits increased only in *L. pinetorum*. Our results show that carbon stored during pre-anthesis plays a key role in reproduction both in annual and perennial *Lesquerella*. The increase in the seed-yield components found with bud removal could potentially reduce longevity in perennial species. The results also show that the number of fruits per plant is a good proxy for seed-yield within a species.

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1. Introduction

Despite the benefits of perennial crop systems and the need for crop diversification, the trade-off between perenniality and seed-yield, predicted by the life history theory (Stearns, 1992) and the low allocation to reproduction usually associated to perennials (Moffat, 1996) are major drawbacks that must be overcome when developing perennial crops. The ecological literature suggests that most perennials produce small amounts of seed relative to their vegetative growth, not as a physiological absolute, but rather as a result of natural selection in a stable, competitive environment favouring longevity (DeHaan et al., 2005).

There is recent evidence that new, promising perennial crops can perform well in semi-arid environments which are unsuitable for the cultivation of more traditional crops (Cox et al., 2002). Among the potential candidates for domestication are annual, biennial, and perennial species of the genus *Lesquerella* (Brassicaceae), with approximately 100 species (Rollins and Shaw, 1973). The present degree of domestication in the genus is incipient, and the focus is currently set on *Lesquerella fendleri*, which has been chosen in the USA as the main candidate for domestication, due to its high seed and oil yield, low seed dormancy, and low fruit dehiscence (Roetheli et al., 1991; Dierig et al., 1993, 1996). Although natural populations of this species have been described as both short-lived perennials (Rollins and Shaw, 1973) and annuals (Barclay et al., 1962; Gentry and Barclay, 1962), the cultivated type of *L. fendleri* behaves strictly as an annual (Dierig et al., 1993; Roseberg, 1993; Ravetta and Soriano, 1998). The feasibility of a perennial crop

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of *Lesquerella* is not yet clear because seed-yield in perennials is usually limited by low harvest indices due to a trade-off between reproductive output and biomass allocated to survival. Increases in seed-yield tend to reduce perenniality (Jackson and Dewald, 1994; Moffat, 1996).

Improved understanding of yield responses to alterations in assimilates availability during different phenological phases has produced major advances in crop physiology and resultant management practices. Assimilated carbon is assigned to different organs (leaves, stems, roots, reproductive organs, etc.) as the result of a set of metabolic and transport processes that govern the flux of energy through a system of sources and sinks (Wardlaw, 1990). In some species, current photosynthesis is the main source of carbon used for seed-set and seed-filling, but carbohydrate reserves can be an important source of energy to sustain these processes when photosynthesis declines due to various kinds of stress, such as drought (Bindingner et al., 1977; Palta et al., 1994), heat stress (Blum et al., 1994) and diseases (Blum, 1998).

The analysis of the generation of seed-yield is a complex process. It has been approached through the determination of main yield components: number of fruits per plant, number of seeds per fruits and seed-weight (Mitchell, 1970; Egli, 1998; Cárcova et al., 2004). The different yield components are set at different ontogenetic stage, which demonstrates that their magnitude depends almost exclusively on the source-sink ratio at that particular moment (Cárcova et al., 2004).

For grain crops in general, it is widely accepted that their yield is limited by sink rather than by source (Patrick, 1988). Studies performed in *Brassica napus* (another Brassicaceae like *Lesquerella*) have shown that an increase in the source-sink relationship, produced by a reduction in the number of flowers, leads to an increase in leaf biomass, which would suggest an increase in photosynthetic rate (Noquet et al., 2004). Experiments in sunflower (*Helianthus annuus* L.) have shown that yield performance can be used as an indicator of source limitation (Andrade and Ferreiro, 1996; Dosio et al., 2000). Although in these experiments the authors did not measure the source-sink ratio, thinning during seed-filling increased the number of filled fruits and dry mass per fruit, whereas shading had the opposite effect. The early evaluation of the source-sink equilibrium of a crop, can offer the chance to adjust both selection programs and agricultural practices of that crop (Bingham et al., 2007).

The objective of this work was to determine the effect of the source-sink ratio on seed-yield and yield components in annual and perennial species of *Lesquerella*. We predict that (i) due to differences in allocation patterns seed-yield and yield components in perennials will be less affected by changes in the source-sink ratio (higher stability) than in annuals and, (ii) since seed-weight has been found to be the most stable yield component in other crops and wild relatives (Harper, 1977), most variation in seed-yield (as a consequence of changes in source-sink ratios) will be determined by changes in the number fruits per plant and the number of seeds per fruit.

2. Materials and methods

2.1. General

A field experiment was conducted from February 20, 2008 to January 15, 2009 in Chubut, Patagonia Argentina (43°14'S, 65°18'W). Mean annual precipitation in this area is 179 mm, mean annual temperature is 13.4 °C, and absolute minimum air temperature is -15.6 °C (Cabrera, 1994).

The experimental design was a completely randomized design with two factors: source-sink ratio and species. We had four

treatments of source-sink relationships applied to four species of *Lesquerella*, two perennial: *L. mendocina* (Phil.) Kurtz (Origin: La Pampa, Argentina) and *L. pinetorum* Wootton and Standley (Origin: Arizona), and two annual species: *L. angustifolia* Wats (Origin: Oklahoma) and *L. gracilis* Wats (Origin: Oklahoma). The seeds used in this experiment belong to lines that have undergone three cycles of selection. The selection criterion for these lines was individual plant seed-yield applied on stands of plants growing in introductory gardens. Seed from each year's selected plants was used to produce the next generation's stands. Selected plants from F1 were used to establish a new plot from which, again, top yielding plants were selected to form the F2. This was repeated for the F3.

Our selected accessions, had a similar degree of variability in those traits evaluated in our experiment (among which is seed-yield) than wild accessions. The coefficient of variation for seed-yield ranged between 0.6 and 1.0 in selected accessions of the four *Lesquerella* species. For four wild accessions growing in introductory plots the variation coefficient ranged between 0.56 and 1.04 (González-Paleo, 2010).

For this experiment, seeds were initially sown in germination-trays filled with soil: peat moss (1:1 by volume) on February 14, 2008 and maintained in a greenhouse until transplanting to the field, 66 days after sowing (DAS; April 21, 2008).

We used either shading (reduction of source) or removal of flower-buds (reduction of sink) to develop a range of source-sink ratios. Four treatments were applied: (1) shading during pre-anthesis: from 90 days after transplanting (DAT) until the moment in which all species had reached anthesis (140 DAT); (2) shading during post-anthesis: from the moment in which all species had reached anthesis (140 DAT) until physiological maturity (190 DAT); (3) removal of flower-buds (sensu Horvitz and Schemske, 1988; McLaughlin, 2003; Sandvik, 2001); half the flowers reaching anthesis each day were removed daily; and (4) untreated control. The main plots were shaded with black mesh cloth stretched above the top of plots on 1m tall metal structures, which excluded 65% of incident solar radiation.

Each treatment was applied to 5 plots (5 replicates). Each plot had 10 plants per species, arranged in two rows placed 0.30 m apart and with a spacing of 0.17 m between plants. During the course of the experiment, total precipitation was 115.5 mm. Additional water was supplied through irrigation during the entire length of the reproductive phase (25 September to March), with a 20-day frequency, because the reproductive period is critical for yield determination, at least in another species of this genus (*L. flenderi*, Puppala et al., 2004), and is also coincident with the dry season in this area. With each irrigation, the top 20 cm layer was taken to saturation. Weeds were removed manually.

2.2. Measurements and observations

Five plants per species and treatment (one per plot) were harvested by the end of the seed-filling period (November 27 and December 17 for annuals and perennials, respectively). Plant biomass was divided into vegetative shoots, roots, seeds, fruits and support structures (structures of the reproductive organs other than seed and fruit), following Ploschuk et al. (2005). Each fraction was dried at 70 °C for 48 h and weighed.

Yield components (seed-yield, number of fruits per plant, number of seeds per fruit and seed-weight) were measured on one plant per plot ($n = 5$). Individual seed-weight was estimated using a sample of 50 seeds per plant.

2.3. Statistical analyses

Two-way ANOVA (species \times source-sink ratio) were used to compare the effects of source-sink manipulations on seed-

Table 1

Source–sink effects on seed–yield per plant and seed–weight. All four species were pooled together since their response to source–sink treatment was not different (no interaction between treatment and species). Different letters indicate significant differences between treatments ($p < 0.05$).

	Source–sink treatments			
	Shading pre-anthesis	Shading post-anthesis	Control	Flower–bud removal
Seed–yield (g^*pl^{-1})	0.08 \pm 0.02a	0.5 \pm 0.11b	1.02 \pm 0.14c	1.51 \pm 0.14d
Seed–weight (g^*50 seed)	0.14 \pm 0.02ns	0.16 \pm 0.02ns	0.18 \pm 0.02ns	0.15 \pm 0.02ns

Table 2

Source–sink effects (Sv = shaded pre-anthesis, Sr = shaded post-anthesis, removal = removal of flower–buds) on number of fruits per plant in four species of *Lesquerella*. For each species different letters indicate significant differences between treatments ($p < 0.05$). Vertical bars = S.E. of the mean.

Number of fruits per plant	Source–sink treatments			
	Shading pre-anthesis	Shading post-anthesis	Control	Flower–bud removal
<i>L. angustifolia</i>	69.75 \pm 15.13a	170.5 \pm 43.51b	245.75 \pm 44.77b	344.4 \pm 43.82c
<i>L. gracilis</i>	78 \pm 22.83a	195.8 \pm 69.9b	280.67 \pm 16.68b	363.17 \pm 52.68c
<i>L. mendocina</i>	27.4 \pm 8.16a	143 \pm 79.61ab	215 \pm 39.76b	217.8 \pm 35.19b
<i>L. pinetorum</i>	71.67 \pm 14.57a	288 \pm 33b	267.7 \pm 21.75b	640.25 \pm 95.13c

Table 3

Source–sink effects (Sv = shaded pre-anthesis, Sr = shaded post-anthesis, removal = removal of flower–buds) on number of seeds per fruit in four species of *Lesquerella*. Different letters indicate significant differences between treatments ($p < 0.05$). Vertical bars = S.E. of the mean.

Number of seeds per plant	Source–sink treatments			
	Shading pre-anthesis	Shading post-anthesis	Control	Flower–bud removal
<i>L. angustifolia</i>	2.38 \pm 0.22a	3.75 \pm 0.31ab	3.19 \pm 0.24ab	3.4 \pm 0.1b
<i>L. gracilis</i>	3.88 \pm 0.33a	9.17 \pm 1.99ab	10.25 \pm 1.39ab	9.38 \pm 1.14b
<i>L. mendocina</i>	2.87 \pm 0.18a	4.25 \pm 1.76ab	6.75 \pm 0.32b	6.11 \pm 0.52b
<i>L. pinetorum</i>	3.08 \pm 0.52a	5.17 \pm 0.79a	5.5 \pm 0.84a	11 \pm 1.18b

yield and yield components. When significant interactions were detected, one-way ANOVA was performed for each species. Tukey's test was used to detect significant differences between factor combinations. To gain more insight into the relative contribution to seed–yield of yield components associated with source–sink ratio, we performed two path analyses to compare the effect of shading pre-anthesis and the effect of flower–bud removal, both relative to the control treatment. The path analyses were performed using AMOS (Arbuckle and Wothke, 1999). The standardized regression coefficients allow an estimation of how a change in one unit standard deviation of one variable affects another variable (also expressed in units of standard deviation), independent of other variables.

3. Results

3.1. Effect of source–sink ratio on seed–yield and yield components.

All four species showed a similar response in seed–yield to source–sink variations. Compared to control plants, the lowest seed–yield was found on plants shaded during pre-anthesis. The highest seed–yield was for plants under the flower–bud removal treatment, and intermediate yields were found on plants shaded post-anthesis ($p < 0.05$, Table 1).

There were differences between species in the total number of fruits per plant in response to source–sink manipulations (i.e. a significant interaction was found between species and source–sink treatments; $p < 0.05$). When plants were shaded pre-anthesis, the number of fruits per plant was the lowest in all four species. In the removal treatment, the largest response was shown by *L. angustifolia*, *L. gracilis*, and *L. pinetorum*. *Lesquerella mendocina* had no response in number of fruits per plant to any of the treatments, except for shading pre-anthesis, which reduced the number of fruits per plant (Table 2).

The response of the number of seeds per fruit to source–sink manipulation also differed between species (significant interaction, $p < 0.05$). In all four species, the number of seeds per fruit was lowest with shading. Flower–bud removal increased the number of seeds per fruit in *L. pinetorum*, whereas the other three species did not show any difference (Table 3). No effect of source–sink ratio was found on seed–weight ($p > 0.05$, Table 1).

3.2. Relative contribution of yield components to seed–yield.

When shading pre-anthesis and control treatments were compared, seed–yield was mainly explained by two variables: the number of fruits per plant and seed–weight (Fig. 1A). The number of fruits per plant also negatively affected seed–yield through indirect effects on the number of seeds per fruit and seed–weight. Still, the indirect negative effect of number of fruits per plant on seed–yield was lower ($\beta = -0.049$) than the direct effect ($\beta = 0.71$; Fig. 1A). The number of seeds per fruit did not explain differences in seed–yield.

The functional relationships between seed–yield and yield components found for the flower–bud removal treatment were the same as those found for shading pre-anthesis. We found a positive and direct effect of the number of fruits per plant and seed–weight on seed–yield (Fig. 1B) and an indirect and negative effect on number of fruits per plant. The indirect effect was lower ($\beta = -0.18$) than the direct effect ($\beta = 0.71$; Fig. 1B).

4. Discussion

Carbon balance is the result of source–sink interactions, which are moderated by a number of factors including the buffering capacity of storage organs, reproductive sink capacity, and hormonal and nutritional control (Wardlaw, 1990). While annual plants invest most of their carbohydrates on seed formation, herbaceous perennials use a proportionally higher amount of carbon to produce roots

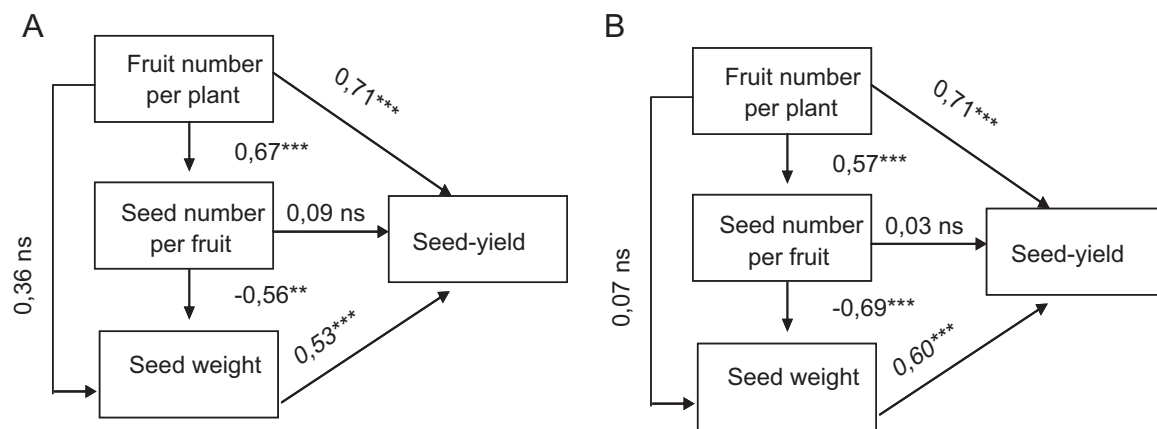


Fig. 1. Path analysis diagram for the four species of *Lesquerella* pooled together, showing the effects of yield components on seed-yield for plants that received: (A) pre-anthesis shading and (B) flower-bud removal. Numbers indicate direct path coefficients between variables. Asterisks indicate significance of the coefficient: *** $p < 0.01$ and ** $p < 0.05$.

and storage organs (Schultz, 1982; Tilman, 1988). This enhanced storage capacity can, in turn provide a source of carbon during periods of stress. Because of these differences in storage reserves and their use, we predicted that when subjected to alterations in source–sink relationships, perennial *Lesquerella* should have more stable yields and less variable yield-components than co-generic annuals. This prediction was also supported by evidence from annual crops differing in storage capacity (Andrade and Ferreiro, 1996).

Against our prediction, we found that both annual and perennial species of *Lesquerella* showed a similar response in seed-yield to a range of source–sink ratios. In all four species, seed-yield decreased with reductions of source pre-anthesis (shading) and increased with flower-bud removal (Table 1). These changes in seed-yield were the result of changes in the number of fruits per plant and the number of seeds per fruit. Similarly to what happened in *Lesquerella*, the reduction of pre-anthesis assimilate supply resulted in yield losses in *Brassica napus* (Tayo and Morgan, 1979; Diepenbrock, 2000) and sunflower (Cantagallo and Hall, 2002). Although we did not explore the mechanisms behind these responses, reductions in pre-anthesis assimilate supplies have been found to change pre-anthesis carbon storage (Gallagher et al., 1975; Snyder et al., 1993) leaf-area development and growth (Kumudini, 2002) and leaf chemical composition (nitrogen and chlorophyll content), all of which could affect the plant's photosynthetic capacity (Ashraf and Bashir, 2003) and final seed-yield.

The response to flower-bud removal was intriguing as seed-yield for these plants was higher than that of controls. Flower-bud removal resulted in increased number of fruits per plant for three species (both annuals and *L. pinetorum*) and in the number of seeds per fruit only in *L. pinetorum* (Tables 1 and 2), which more than compensated final seed-yield. A number of compensatory mechanisms have been shown for similar responses in other plant species. For example, an increase in the sink, both by an increase in the number or in the activity of the sinks, could cause an increment in the photosynthetic rate (Gifford and Evans, 1981; Mooney and Chiariello, 1984; Watson and Casper, 1984; Garnier, 1991). Also, a transient increase in the source–sink ratio caused by flower-bud removal could result in an increase in leaf area index and leaf growth during seed-filling (Rood et al., 1984; Kumudini, 2002), which translates into enhanced carbon gain induced by sink enlargement. However, in perennials, seed-yield over-compensation could also be supported by carbohydrate reserves. This response could potentially reduce the plants longevity, since reserves would no longer be available for future

re-growth. Seed-yield over-compensation was found in *L. pinetorum* but not in *L. mendocina* suggesting potential differences between these two perennials in the hierarchical importance of allocation patterns to perpetuation organs, storage reserves, and seed. These results agree with previous reports (González-Paleo and Ravetta, 2011) that show that *L. mendocina* has a life-history strategy typical of a perennial, while *L. pinetorum*, even behaving as a perennial, has many traits commonly found in annuals. The mechanisms behind these responses should be further evaluated, especially the understanding of the relative importance of carbon reserves, current photosynthesis and carbon partition in determining yield components, and future yield and plant longevity.

The analysis of yield components has been used to produce more efficient breeding programs (Egli, 1998). Selection to increase one component has not always resulted in seed-yield increases, due to compensatory effects between yield components (Miralles and Slafer, 1995). The analysis of the existence of negative relationships among different yield components could facilitate the selection of indirect criteria to increase seed-yield. To elucidate the indirect (i.e. compensatory effects) and direct effects of yield components on seed-yield variation, we performed a path analysis (Fig. 1). We found compensatory effects between yield components. For example, we detected a direct negative relationship between the number of seeds per fruit and seed-weight, and an indirect negative relationship between the number of fruits per plant and seed-weight through the number of seeds per fruit. Still, this effect was less relevant for seed-yield than the direct effect of the number of fruits per plant. While the number of seeds per fruit changed with source–sink ratios (Table 3), the relationship between this component and seed-yield was not significant in the path analysis. So, against our prediction, the number of seeds per fruit did not explain seed-yield. Also, although the positive relationship between seed-weight and seed-yield was significant, the source–sink ratio did not affect this component. Seed-weight was the more stable yield component, a result that supports our prediction. These results agree with other reports in several crops (Slafer and Savin, 1994; Haro et al., 2008) which show a high degree of homeostasis in seed-weight despite variation in assimilate availability.

Finally, in spite of compensatory effects, we found that the number of fruits per plant is a good proxy for seed-yield in these four species of *Lesquerella* and that it could be used as an indirect selection criterium to increase seed-yield in breeding programs. The number of seeds per fruit and seed-weight are relatively less plastic and probably not as useful as selection traits.

5. Conclusions

Changes in seed-yield and yield components that resulted from the manipulation of the source–sink ratios were independent of the plants life-cycle. In all four species, seed-yield decreased with pre-anthesis shading and increased with flower-bud removal. Our results show that carbon-gain during the rosette stage may be relatively more important for seed-yield than actual assimilation during reproduction, which means that carbon storage plays a key role in reproduction, both in annual and perennial *Lesquerella*.

On the other hand, the increase in the seed-yield components (number of fruits per plant, number of seeds per fruit) found with bud removal (compensatory fruiting) could potentially reduce longevity in perennial species, although it may also come from an increase in carbon gain induced by sink enlargement. The mechanisms behind these responses should be further evaluated, especially the understanding of the relative importance of carbon reserves, current photosynthesis and carbon partition in determining yield components, and future yield and plant longevity.

Changes in seed-yield were due mainly to variations in the number of fruits per plant. Although the number of seeds per fruit responded to source–sink ratios, this yield component was not directly responsible for seed-yield. As predicted, seed-weight showed a high degree of homeostasis despite variation in assimilates availability.

We found compensatory effects among yield components (i.e. number of seeds per fruit and seed-weight and number of fruits per plant and seed-weight) that could reduce selection progress for higher seed-yield through the use of yield components as indirect criteria. Still, this compensatory effect was less important than the direct effect of the number of fruits per plant on seed-yield. We propose that the number of fruits per plant is a good proxy for increase seed-yield in these four species of *Lesquerella* and that it could be used as an indirect selection criterion in breeding programs.

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