

# Development of New Perennial Oil-Crops for Marginal Environments: Productivity of *Lesquerella mendocina* under Different Nitrogen Availability

Edmundo L. Ploschuk\* • Liliana B. Windauer

Cátedra de Cultivos Industriales. Facultad de Agronomía. Universidad de Buenos Aires. Av. San Martín 4453 (1417) Buenos Aires, Argentina

Corresponding author: \* ploschuk@agro.uba.ar

## ABSTRACT

Several reports are in agreement with the fact that perennial grain yields do not match of the analog annual species, but others revealed that the perennials may be high. Not enough knowledge about the impact of nutritional conditions on the maintenance of yield stability along different growing seasons is available for perennial grain crops. *Lesquerella mendocina* is a promising species native from Argentina that produces oil with hydroxy fatty acids (HFA) in the seeds. The objective of this work was to test the hypothesis that seed production and yield components during the second year do not decrease in *L. mendocina* under optimal N availability. An experiment was carried out outdoors during two consecutive years. In 2004, treatments consisted of a control under optimal N availability measured during the first growing season (LM1-1), and two treatments which plants remained fertilized during the first year and analyzed during the second growing season (LM2) under low (N-) and high (N+) N availability. In 2005, two additional N- and N+ treatments were applied (LM1-2) in order to compare the production in the first season with LM2 plants. Similar yields were found for LM2 N+ than those for LM1-1 and LM1-2 N+, despite the drastic reduction of plant density in the former. Higher individual seed yield and inflorescence peduncles compensated the lack of plant stand. LM2 yield was more affected by N availability than LM1-2, while no changes in seed allocation were produced by N either plant age. The results suggest that *L. mendocina* performs as a promissory species with stable yields along years if future breeding programs improve seed allocation and resistance to fungal diseases.

**Keywords:** new crops, nutrient availability, oil-seed crops, perennial grain crops, semiarid lands, sustainability

**Abbreviations:** HFA, hydroxy fatty acids; N, nitrogen; PM, physiological maturity

## INTRODUCTION

Annual grain crops have dominated the agricultural landscape since the time of the earliest farmers 10,000 years ago (Cox *et al.* 2002). The increasing demand to expand food production under an increasing human population lead to the development of plant breeding programs for annual grain crops aimed at increasing grain yields. In this context, maximization of potential yield would have contributed to the discarding of several morphological and physiological traits that could be critical for the improvement of crop survival and stability under environmental limitations (Ceccarelli and Grando 1996). The introduction of perennial grain crops has been proposed to reduce soil erosion in agricultural systems, and breeding methodologies have already been described for at least twenty perennial grain species (Cox *et al.* 2002; Glover 2003). Breeders have the genetic resources for breeding perennial grains, but the possibility of a tradeoff between potential grain yield and perenniality (Jackson and Jackson 1999) has been posed as a limitation to its progress.

Several reports for many grain crop species are in agreement with the fact that perennial grain yields are not as high as those for the analog annual species (Wagoner 1990). However, other studies revealed that grain yields may be high in perennial Sorghum (Piper and Kulakow 1995), and seed production can be increased without compromising the vegetative biomass invested in sustaining perenniality (Moffat 1996; Pimm 1997). In addition, other alternative perennial crops such as Illinois bundleflower (*Desmanthus illinoensis*) and wild senna (*Cassia marilandica*), yielded up to 2000 Kg/ha (Piper 1998; Fischbach *et*

*al.* 2005).

Another important concern related to the performance of perennial grain crops is associated with the stability of yield along the different years. Unfortunately, evidence in perennial wheat suggests that yield could perform satisfactorily only in the year in which the crop is established from seed, while production is drastically reduced at the subsequent reproductive periods (Suneson *et al.* 1963; Tsitsin 1965; Cox *et al.* 2006). Not enough knowledge about the impact of nutritional conditions on the maintenance of yield stability along the different growing seasons is available for perennial grain crops, however.

The genus *Lesquerella* (Brassicaceae) is a potential industrial crop due to the HFA in its seeds (Dierig *et al.* 1993). It includes approximately 100 species with annual, biennial and perennial habits (Rollins and Shaw 1973). *Lesquerella fendleri* (A. Gray) S. Watson is a candidate for domestication because of its high seed and oil yield, low seed dormancy, and low fruit dehiscence (Roetheli *et al.* 1991). Although the natural populations of this species have been described as short-lived perennial (Rollins and Shaw 1973) and annual (Barclay *et al.* 1962), the cultivated types are cropped as an annual (Dierig *et al.* 1993) and behaves strictly as an annual in Argentina (Ploschuk *et al.* 2001). No perennial structures were found in this species, and all stems bear reproductive structures at flowering including the apical meristem (Windauer 2002; Ploschuk *et al.* 2003).

Thus, environmental and cultural effects on the growth and yield in annual crop systems of *Lesquerella* sp., have been reported for N (Nelson *et al.* 1996, 1999; Ploschuk *et al.* 2005), sowing date and plant density (Brahim *et al.* 1996; Rodriguez Garcia *et al.* 2007), water availability



Fig. 1 *Lesquerella mendocina* plant growing during the first (A) and second (B) growing season.

(Puppala *et al.* 1997; Ploschuk *et al.* 2001; Puppala *et al.* 2005), salinity (Grieve *et al.* 1997; Dierig *et al.* 2003), phenology (Windauer *et al.* 2004, 2006), germination (Adam *et al.* 2007; Windauer *et al.* 2007) and temperature (Dierig *et al.* 2006; Alvarez Prado and Ploschuk 2008).

Alternatively, other species of the genus such as the perennial native from Argentina *L. mendocina* (Phil.) Kurtz (Cabrera 1967; Correa 1984), could be developed as a source of HFA in regions with cool temperatures and arid or semi-arid lands (Ploschuk *et al.* 2001, 2003, 2005). In contrast to *L. fendleri*, *L. mendocina* develops perennial rosettes with lateral spicate inflorescences every year, including the first year of establishment (Fig. 1). This trait could contribute to increased crop stability (across sites and years), making *L. mendocina* a promising perennial alternative to *L. fendleri* for sustainable systems in marginal environments.

Previous studies revealed that *L. mendocina* first-year yields were similar to those of *L. fendleri* (Ploschuk and Ravetta 2003; Ploschuk 2005; Ploschuk *et al.* 2005). Greater root and vegetative shoot allocation in the former species were counterbalanced by a lower allocation to non seed reproductive structures compared to the latter. However, little is known about the performance of perennial grain crops such as *L. mendocina* during the years following sowing and the effect of nutrient availability during this period. The objective of this work is to test the hypothesis that seed production and yield components during the second year do not decrease in *L. mendocina* under optimal N availability.

## MATERIALS AND METHODS

### Plant handling and treatments

An experiment was carried out under field conditions, during 2004 and 2005 at the Facultad de Agronomía, Universidad de Buenos Aires, Argentina (34° 35' S, 58° 29' W) on a salty clay loam soil (Vertic Argiudoll). Seeds of *L. mendocina* were collected from a native stand at Lihuel Calel, La Pampa, Argentina (37° 57' S, 65° 33' W) and previously multiplied in plots at the Facultad de Agronomía. The experiment was arranged in three randomized complete blocks with five treatments. Each replicate consisted of a plot with eight rows, 0.2 m apart and 1 m long for a total initial plant density of 50 plants m<sup>-2</sup>. Plants were grown under adequate water conditions and kept free from weeds by manual removal. Cipermin (Cipermetrine 25%, 20 cm<sup>3</sup> hl<sup>-1</sup>) and Zineb Azul Brometan (Zineb 70%, 20 g hl<sup>-1</sup>) were applied at monthly intervals to prevent damage from insects and fungi, respectively.

The experiment was sown on June 4 2004 (Fig. 2). In this year, the sown treatments consisted of a *L. mendocina* control under optimal N availability analyzed and harvested during the first growing season (LM1-1), and two treatments which plants remained fertilized during the first year and were analyzed during the second growing season (LM2) under low (N-) and high (N+) N availability. In 2005 (sowing date June 3), two additional N- and N+ treatments were arranged (LM1-2) in order to compare under the same environmental conditions plants producing seeds under the first and the second growing season. Sowing date was chosen in order to maximize the synchronization of the flowering phase between LM1-2 and LM2 treatments (Ploschuk *et al.* 2005). Nitrogen fertilization consisted of urea applications (150 Kg of N ha<sup>-1</sup>) applied before sowing for LM1-1, LM2 N+, LM2 N- in 2004. The same dose was also applied in 2005 for LM1-2 N+ before sowing and for LM2 N+ at the same date, while LM1-2 N- and LM2 N- remained unfertilized.

### Seed yield and relative allocation

Four plants per block were harvested after PM (when fruits were dehiscent at touch and contained reddish seeds, see Fig. 2), and plant biomass was divided into vegetative shoots (leaves and stems), roots, seeds and non-seed reproductive biomass (inflorescence peduncles and siliques). Samples were dried at 70°C for at least 48 h and weighed. The dry weights of the different fractions were measured for each treatment. Previous studies revealed that seed-oil concentrations were around 20% and the patterns of variation in carbon content measured as glucose equivalents were similar to those for biomass in all vegetative and reproductive organs (Penning de Vries *et al.* 1974; Ploschuk 2005). Thus, relative allocations to vegetative and reproductive organs (Bazzaz and Ackerly 1992) were made using biomass as a representative currency for carbon units. When LM2 plots in their first year reached PM, all reproductive fractions (seeds and non-seed reproductive organs) were removed, in order to ensure that the reproductive biomass harvested the following year was entirely produced during this second season. Relative allocations (percentage of total biomass) for LM2 plants were calculated in terms of the dry mass produced during the second year. Thus, mean vegetative

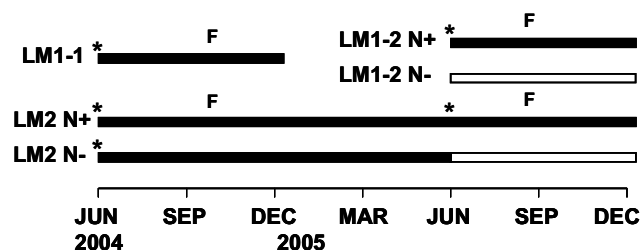


Fig. 2 Scheme of the treatments arranged in the experiment. Horizontal bars indicate the period between sowing and harvesting after physiological maturity, under high (solid bars) and low (empty bars) nitrogen availability. Asterisks indicate the moment when fertilization was applied. F = Onset of flowering.

shoot and root biomass were estimated by the difference between the mean biomass harvested at the end of the second year (LM2) and the mean biomass from LM1-1 plants. Yield measurements ( $\text{Kg ha}^{-1}$ ) were estimated by harvesting the entire plot at PM.

### Plant density and phenology

The number of inflorescence peduncles was measured on four plants per block at harvesting for each treatment. No significant change in plant density was detected during the first reproductive cycle until PM (LM1-1 and LM1-2 plants, data not shown). In LM2 plants, a measurement of plant density ( $\text{plants m}^{-2}$ ) was made at PM in 2005, in order to estimate plant mortality during the second growing season.

### Statistical analyses

Analyses of variance were performed for yield, biomass allocation and phenology, using the InfoStat software (Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina). When significant differences were found, Tukey's test was conducted to detect significant differences among the factor combinations ( $P < 0.05$ ). Natural logarithm transformations were performed when variance differed between treatments, while arcsine  $\sqrt{x}$  transformations were made for relative allocation measurements.

## RESULTS

### Seed yield

The onset of flowering (plots with at least one plant flowered) was September 25, 2004 for LM1-1, August 26, 2005 for LM1-2 and August 28, 2005 for LM2 plots (Fig. 2). Yields of around  $400 \text{ kg ha}^{-1}$  were produced by plants under high N availability during the first growing season, both for plants sown during the first (LM1-1) and second (LM1-2 N+) year (Fig. 3). Similar yields were obtained for fertilized plants during the second growing season (LM2 N+). Under low N availability, yield reductions were found for LM1-2 N- and LM2 N- plants. However, the reduction was higher for the later treatment during the second growing season, reaching 75% of that for fertilized plants ( $P < 0.05$ ).

Plant density was drastically reduced by plant mortality during the second growing season ( $11.5 \pm 0.73 \text{ pl m}^{-2}$  and  $12.8 \pm 0.70 \text{ pl m}^{-2}$  for LM2 N+ and LM2 N- plants respectively), representing a reduction of around 75% respect to the  $50 \text{ pl m}^{-2}$  established by LM1-1 and LM1-2 plots. This mortality was not associated with senescence processes related with the grain filling process during the previous season, but with fungal diseases during the second growing season (data not shown). Thus, different patterns were found when seed yield was analyzed per plant (Fig. 4). Greater individual seed yields near  $4 \text{ g plant}^{-1}$  were reached by LM2 N+ plants compared to plants growing during its first season under high N availability (LM1-1, LM1-2 N+). Significant reductions under low N availability around 37% and 57% were detected for both LM1-2 N- and LM2 N- plants respectively ( $P < 0.05$ ). However, individual seed yield in LM2 N- plants was similar to that measured under high N availability in the first growing season (LM1-1 and LM1-2 N+).

### Plant phenology

The number of inflorescence peduncles was similar for plants growing in their first reproductive cycle during 2004 (LM1-1) and 2005 (LM1-2) (Fig. 5). This variable was significantly higher for plants flowering during the second growing season (LM2), reaching 95 inflorescence peduncles per plant for the N+ treatment ( $P < 0.05$ ). On the other side, significant reductions of up to 50% of the number of inflorescences were found for LM2 plants under low N availability ( $P < 0.05$ ), while no significant changes in LM1-2 N- plants were detected by this limitation. However, even under low N availability, inflorescence peduncles in

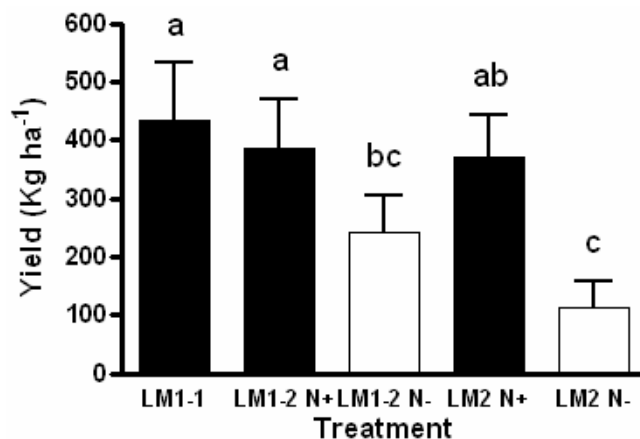


Fig. 3 Seed yield ( $\text{Kg ha}^{-1}$ ) for *Lesquerella mendocina* during the first growing season (LM1-1), second growing season (LM2) and first growing season sown in the second year (LM1-2) for fertilized (N+) and non fertilized (N-) treatments. Error bars indicate standard errors ( $n = 3$ ). Different letters indicate significant differences between treatments ( $P < 0.05$ ).

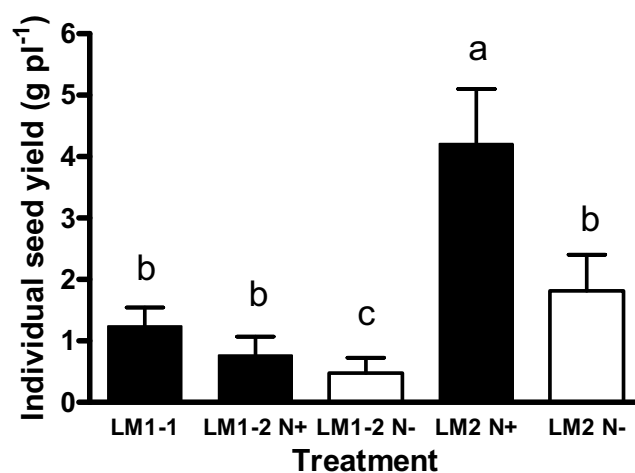


Fig. 4 Individual seed yield ( $\text{g plant}^{-1}$ ) for *Lesquerella mendocina* during the first growing season (LM1-1), second growing season (LM2) and first growing season sown in the second year (LM1-2) for fertilized (N+) and non fertilized (N-) treatments. Error bars indicate standard errors ( $n = 9-12$ ). Different letters indicate significant differences between treatments ( $P < 0.05$ ).

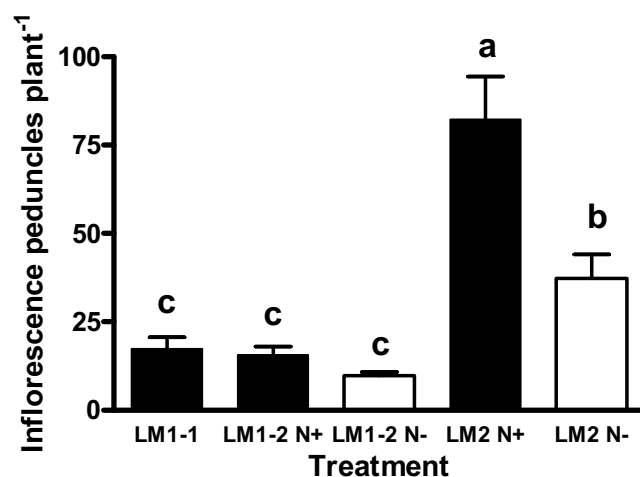
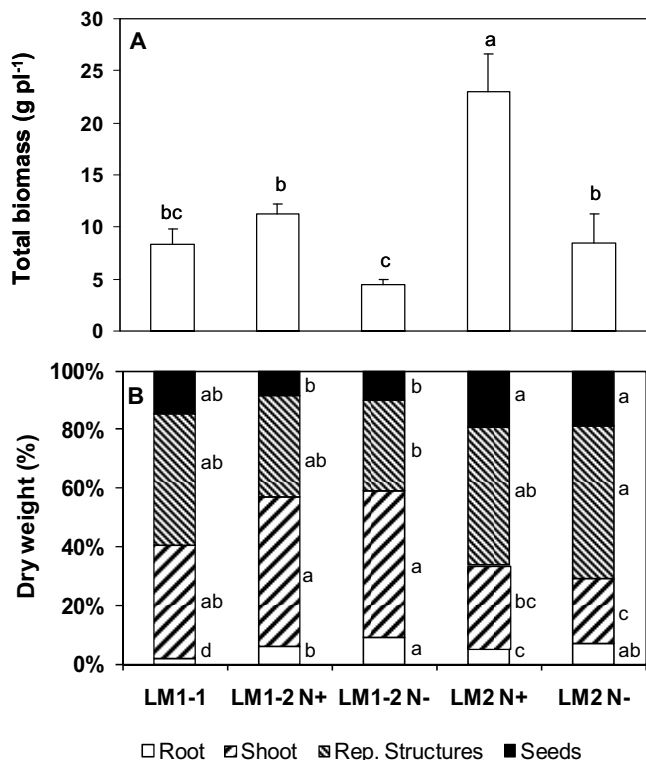


Fig. 5 Number of inflorescence peduncles per plant for *Lesquerella mendocina* during the first growing season (LM1-1), second growing season (LM2) and first growing season sown in the second year (LM1-2), measured at harvesting after PM for fertilized (N+) and non fertilized (N-) treatments. Error bars indicate standard errors ( $n=9-12$ ). Different letters indicate significant differences between treatments ( $P < 0.05$ ).



**Fig. 6** Total biomass (g plant<sup>-1</sup>) for the entire plant (A) and relative biomass allocation (% of total plant biomass) to the different fractions for *Lesquerella mendocina* (B) during the first growing season (LM1-1), second growing season (LM2) and first growing season sown in the second year (LM1-2) for fertilized (N+) and non fertilized (N-) treatments. Biomass and allocations for LM2 were calculated in terms of produced during the second year. Error bars indicate standard errors (n = 9-12). Different letters indicate significant differences between treatments for each fraction ( $P < 0.05$ ).

LM2 N- plants were higher than that for the high N availability treatment measured in the first growing season (LM1-1 and LM1-2 N+).

### Biomass production and allocation

Results for total plant biomass produced by the different treatments had a similar pattern to individual plant seed yield (compare Fig. 6A with Fig. 4). As a consequence, no significant changes in relative biomass allocation for seeds were found between plants flowered during their first flowering cycle, both for the first (LM1-1) and the second (LM1-2) year of treatments, although allocation to roots was higher in the latter (Fig. 6B). Independently of N availability, allocation to seeds was higher in the LM2 treatment than that for the first reproductive period in LM1-2 plants, growing in the same season under the same environmental conditions ( $P < 0.05$ ). A higher allocation to non-seed reproductive structures was also found for LM2 N- plants as compared to that observed for the LM1-2 N- treatment ( $P < 0.05$ ). These patterns were associated with a higher allocation to roots and shoot in LM1-2 plants, as compared to that observed for the LM2 treatment ( $P < 0.05$ ). However, seed allocation for the same crop flowered during the previous year (LM1-1) did not differ from LM2 plants, although it tended to be lower in the former.

In general terms, high N availability (N+ treatment) did not affect relative allocation to seeds compared to plants under low N conditions (N- treatment) in both LM1-2 and LM2 plants, but did result in decreased allocation to roots relative to N- treatments ( $P < 0.05$ ). Although no significant changes were found for allocation to shoot and non-seed reproductive structures, tendencies show that the lower allocation to roots in N+ treatments was produced at ex-

penses of a higher allocation to some of these biomass fractions.

### DISCUSSION

Under optimal N availability, yield in *L. mendocina* during the second reproductive cycle did not decrease from that produced during the first season. Yield (Kg ha<sup>-1</sup>) was maintained even under the drastic reduction in plant density of 75% resulting from plant mortality with respect to the 50 pl m<sup>-2</sup> established during the first flowering cycle. Yields were maintained by a great increase in individual seed yield and the number of inflorescence peduncles. These results contrast with the drastic reductions reported for perennial wheat during the second year of establishment (Suneson *et al.* 1963; Tsitsin 1965; Cox *et al.* 2002). Thus, our results are in agreement with the hypothesis that seed production and yield components during the second year do not decrease in *L. mendocina* under optimal N availability.

The performance of *L. mendocina* have been tested in Argentina by comparative experiments with the candidate species *L. fendleri* (Ploschuk *et al.* 2003; Ploschuk and Ravetta 2003; Ploschuk 2005; Ploschuk *et al.* 2005). These studies revealed that yields and reproductive allocations were similar between the two species when managed as annual crops, but no information was available about yields during subsequent growing seasons under different nutrient availability. Previous reports in other herbaceous species detected meristem limitations and apical dominance associated with the vegetative perpetuation organ (rosette) of the perennial (Watson 1984; Geber 1990; Bazzaz and Ackerly 1992; Obeso 2002). The results obtained in this work corroborate the capacity of *L. mendocina* to generate a great number of inflorescence peduncles during the second growing season. This effect was exacerbated by the drastic reduction in plant density produced in our experiment by plant mortality, and is in accordance with the idea that a perennial grain crop could perform well under optimal environmental conditions, at least during the second year. Further research is needed to investigate the causes of plant mortality and to analyze the performance of this species as a perennial crop under optimal plant densities.

Low levels of N availability resulted in decreased yields of *L. mendocina* both under its first (LM1-2 N-) and second (LM2 N-) reproductive cycle by 37% and 75% respectively compared to their respective N+ treatments (Fig. 3). The greater reductions of LM2 N- plants could be in part attributed to the low plant density with respect to that for LM1-1 plants. However, a similar pattern was found for individual seed yield (37% for LM1-2 N- and 57% for LM2 N-, Fig. 4). This effect was clearly associated with the pattern found for the number of inflorescence peduncles produced per plant (Fig. 5). In contrast, no changes in seed allocation were produced by N availability. The impact of N was fundamentally affected on total plant biomass and no significant changes in allocation to the different biomass fractions were produced by the low N availability, with the exception of the higher allocation to roots (Fig. 6). Lower productivities under low N availability were reported for the total biomass production of alternative perennial species for bio-fuel production, such as miscanthus (*Miscanthus x giganteus* Greef et Deu.) and switchgrass (*Panicum virgatum* L.) (Boehmel *et al.* 2008). These results are also in agreement with previous measurements done during the first growing season (Ploschuk *et al.* 2005). Thus, the results show that the negative impact of N availability on yield was higher in the oldest plants, although the pattern of seed allocation was not affected by the treatment.

Allocation to seeds during the second growing season did not differ from that observed during the previous year (LM1-1 plants). Lower allocation, however, was found in LM1-2 plants under the same meteorological conditions than LM2 plants, as a consequence of the higher allocation to shoot produced in the former (Fig. 6). The higher productivity of total biomass in LM2 plants under optimal N

conditions contrasts with the low values found by Ploschuk *et al.* (2005) in non fertilized plots during the second growing season. In general terms, seed-allocation reported here was lower than that found for major grain crops (Lopez Pereira *et al.* 2000; Vega *et al.* 2000) possibly reflecting the lack of selection on *L. mendocina*. Great efforts in future plant breeding programs will be needed in order to improve harvest index and yield in this species.

Related to the previous comments, the highest yields obtained in this work under high N availability of around 400 kg ha<sup>-1</sup> are low with respect to that expected for a grain crop. Although these values were similar to those obtained for *L. fendleri* under similar conditions (Ploschuk and Ravetta 2003; Ploschuk 2005), yields up to 2000 kg ha<sup>-1</sup> were obtained for the same germplasm in the latter species in Arizona (Dierig *et al.* 1993; Thompson and Dierig 1994). Besides the lack of breeding on *L. mendocina*, three other possible explanations of the lower yields could be related to environmental factors: i) the later sowing date for LM1-1 and LM1-2 plots (chosen to maximize the synchronization of the flowering phase between LM1-2 and LM2 treatments) ii) the lower initial plant density used compared to those reported by other studies (Brahim *et al.* 1996; Rodriguez Garcia *et al.* 2007) and iii) the climatic conditions of the site where the experiment was performed. In addition, the extremely low density reached by LM2 treatments discard the possibility to compare yields under the same density with those of plants in their first reproductive cycle. Notwithstanding, our experiment allowed us to reveal the potential of *L. mendocina* to develop high individual seed yields plant<sup>-1</sup>, as a consequence of a high number of inflorescence peduncles. Although no radiation interception measurement was done in this experiment, visual observations reveal that less than 50% of the incident radiation was intercepted by the crop in LM2 plots, suggesting that yields could have been higher under normal densities without important increases in plant competition.

Finally, previous studies revealed that a selection breeding program could be successful in *L. mendocina*, since an increase of seed allocation may be produced at expense of secondary reproductive structures, instead of the perpetuation organ (Ploschuk *et al.* 2005). Although it is usually believed that selection for higher yields should shorten the plant's lifespan in accordance with the phenotypic trade-off model, recent research suggests that environmental and genetic changes can result in increases in both lifespan and yield simultaneously (DeHaan *et al.* 2005). In the case of *L. mendocina*, plant mortality was not due to the above mentioned trade-off but to fungal diseases that might be overcome by breeding programs. Even in the case that seed yield in a perennial crop was lower than that expected for a traditional annual crop, this could have a number of advantages for improving the sustainability of the vast extension of semiarid lands and marginal environments in Argentina, as the ones reported for the use of perennial crops in the Australian dryland agricultural systems (Bell *et al.* 2008).

## CONCLUSIONS

Our work shows that *L. mendocina* could maintain yield stability during the second year under high N availability, in spite of the drastic reduction in plant density, by a great compensation of individual seed yield associated with the higher number of inflorescences, relative to those produced during the first growing season. Low N availability decreased yield and individual seed yield and the effect was more emphasized during the second growing season, although no changes in seed allocation were produced by N. The results suggest that yield could be clearly higher during the second growing season if plant stand could be maintained, and further breeding programs are needed in order to reduce plant mortality by fungal diseases and to improve allocation to seeds. Hence, *L. mendocina* performs as a promising species to be developed as a perennial crop for semiarid lands such as the vast marginal environments in Argen-

tina.

## ACKNOWLEDGEMENTS

This work was supported by funding from the Agencia Nacional de Promoción Científica y Tecnológica (PICT 1617) and the Universidad de Buenos Aires (UBACyT G008). We thank Diego Fernandez Abejón for his assistance in the field and Daniel Bertero and Jerry Glover for critical review of the manuscript. We also thank the Administración Nacional de Parques Nacionales for allowing us to collect *L. mendocina* seeds from natural populations.

## REFERENCES

- Adam NR, Dierig DA, Coffelt TA, Wintermeyer MJ, Mackey BE, Wall GW (2007) Cardinal temperatures for germination and early growth of two *Lesquerella* species. *Industrial Crops and Products* **25**, 24-33
- Alvarez Prado AF, Ploschuk EL (2008) Development and growth of two *Lesquerella* species grown under different temperatures during the reproductive period. *Industrial Crops and Products* **27**, 400-403
- Barclay AS, Gentry HS, Jones Q (1962) The search for new industrial crops. II: *Lesquerella* (Cruciferae) as a source of new oilseeds. *Economic Botany* **16**, 95-100
- Bazzaz FA, Ackerly D (1992) Reproductive allocation and reproductive effort in plants. In: Fenner M (Ed) *Seeds: The Ecology of Regeneration in Plant Communities*, C.A.B. International. Wallington, Oxford, pp 1-26
- Bell LW, Byrne F, Ewing MA, Wade LJ (2008) A preliminary whole-farm economic analysis of perennial wheat in an Australian dryland farming system. *Agricultural Systems* **96**, 166-174
- Boehmel C, Lewandowski I, Claupein W (2008) Comparing annual and perennial energy cropping systems with different management intensities. *Agricultural Systems* **96**, 224-236
- Brahim K, Stumpf DK, Ray DT, Dierig DA (1996) *Lesquerella fendleri* seed oil content and composition: Harvest date and plant population effects. *Industrial Crops and Products* **5**, 245-252
- Cabrera AL (1967) *Flora de la Provincia de Buenos Aires* (Vol 4), Colección Científica INTA. Buenos Aires, Argentina, 671 pp
- Ceccarelli S, Grando S (1996) Drought as a challenge for the plant breeder. *Plant Growth Regulation* **20**, 149-155
- Correa MN (1984) *Flora patagónica. IV a: Salicaceae a Cruciferae* (Vol 8), Colección Científica INTA. Buenos Aires, Argentina, 559 pp
- Cox TS, Bender M, Picone C, Van Tassel DL, Holland JB, Brummer EC, Zoeller BE, Paterson AH, Jackson W (2002) Breeding perennial grain crops. *Critical Reviews in Plant Science* **21**, 59-91
- Cox TS, Glover JD, Van Tassel DL, Cox CM, DeHaan LR (2006) Prospects for developing perennial grain crops. *BioScience* **56**, 649-659
- DeHaan LR, Van Tassel DL, Cox TS (2005) Perennial grain crops: A synthesis of ecology and plant breeding. *Renewable Agriculture and Food Systems* **20**, 5-14
- Dierig DA, Thompson AE, Nakayama FS (1993) *Lesquerella* commercialization efforts in the United States. *Industrial Crops and Products* **1**, 289-293
- Dierig DA, Grieve CM, Shannon MC (2003) Selection for salt tolerance in *Lesquerella fendleri* (Gray) S. Wats. *Industrial Crops and Products* **17**, 15-22
- Dierig DA, Adam NR, Mackey BE, Coffelt TA (2006) Temperature and elevation effects on plant growth, development, and seed production of two *Lesquerella* species. *Industrial Crops and Products* **24**, 17-25
- Fischbach JA, Peterson PR, Sheaffer CC, Ehlike NJ, Byun J, Wyse DL (2005) Illinois bundleflower forage potential in the upper midwestern USA: I. Yield, regrowth, and persistence. *Agronomy Journal* **97**, 886-894
- Geber MA (1990) The cost of meristem limitation in *Polygonum arenastrum*: Negative genetic correlations between fecundity and growth. *Evolution* **44**, 799-819
- Glover J (2003) Characteristics and impacts of annual vs. perennial systems. *Proceedings of Sod-Based Cropping System Conference*, North Florida Research and Education Center-Quincy, University of Florida, pp 1-6
- Grieve CM, Poss JA, Donovan TJ, Francois LE (1997) Salinity effects on growth, leaf-ion content and seed production of *Lesquerella fendleri* (Gray) S. Wats. *Industrial Crops and Products* **7**, 69-76
- Jackson W, Jackson LL (1999) Developing high seed yielding perennial polycultures as a mimic of mid-grass prairie. In: LeFroy R, Lefroy EC, Hobbs RJ, O'Connor MH, Pate JS (Eds) *Agriculture as a Mimic of Natural Ecosystems*, Kluwer Academic Publishers, Netherlands, pp 1-37
- Lopez Pereira M, Trapani N, Sadras VO (2000) Genetic improvement of sunflower in Argentina between 1930 and 1995 - Part III. Dry matter partitioning and grain composition. *Field Crops Research* **67**, 215-221
- Moffat AS (1996) Agricultural research - Higher yielding perennials point the way to new crops. *Science* **274**, 1469-1470
- Nelson JM, Dierig DA, Nakayama FS (1996) Planting date and nitrogen fertilization effects on *Lesquerella* production. *Industrial Crops and Products* **5**, 217-222
- Nelson JM, Watson JE, Dierig DA (1999) Nitrogen fertilization effects on *Lesquerella* production. *Industrial Crops and Products* **9**, 163-170

- Obeso JR** (2002) The costs of reproduction in plants. *New Phytologist* **155**, 321-348
- Penning de Vries FWT, Brunsting AHM, van Laar HH** (1974) Products, requirements and efficiency of biosynthesis: A quantitative approach. *Journal of Theoretical Biology* **45**, 339-377
- Pimm SL** (1997) In search of perennial solutions. *Nature* **389**, 126-127
- Piper JK, Kulakow PA** (1995) Seed yield and biomass allocation in *Sorghum bicolor* and F1 and backcross generations of *S. bicolor* x *S. halepense* hybrids. *Canadian Journal of Botany* **72**, 468-474
- Piper JK** (1998) Growth and seed yield of three perennial grains within monocultures and mixed stands. *Agricultural Ecosystems and Environment* **68**, 1-11
- Ploschuk EL, Windauer L, Ravetta DA** (2001) Potential value of traits associated with perennial habit in the development of new oil-seed crops for arid lands. A comparison of *Lesquerella fendleri* and *L. mendocina* subjected to water stress. *Journal of Arid Environments* **47**, 373-386
- Ploschuk EL, Cerdeiras G, Windauer L, Dierig DA, Ravetta DA** (2003) Development of alternative *Lesquerella* species in Patagonia (Argentina): Potential of *Lesquerella angustifolia*. *Industrial Crops and Products* **18**, 1-6
- Ploschuk EL, Ravetta D** (2003) Annual and perennial *Lesquerella* subjected to water stress during seed-filling. *The Association for the Advancement of Industrial Crops International Conference*, Portland, Oregon, USA. Available online: <http://www.aaic.org/03progrm.htm>
- Ploschuk EL** (2005) Influencia de la perennidad y la dinámica floral sobre el costo reproductivo en *Lesquerella* sp. - Potencial cultivo oleaginoso para zonas áridas de secano. PhD thesis. Escuela para Graduados de la Facultad de Agronomía, Universidad de Buenos Aires, Argentina, 85 pp
- Ploschuk EL, Slafer GA, Ravetta D** (2005) Reproductive allocation of biomass and nitrogen in annual and perennial *Lesquerella* crops. *Annals of Botany* **96**, 127-135
- Puppala N, Fowler J, Dierig DA, Dahlquist G** (1997) Oil content and fatty acid composition of *Lesquerella fendleri* in response to timing and duration of moisture stress. *International Conference of the AAIC*, Saltillo, Mexico. Available online: <http://www.aaic.org/97program.htm>
- Puppala N, Fowler JL, Jones TL, Gutschick VP, Murray L** (2005) Evapotranspiration, yield and water-use efficiency responses of *Lesquerella fendleri* at different growth stages. *Industrial Crops and Products* **21**, 33-47
- Rodriguez Garcia R, Jasso de Rodriguez D, Angulo-Sanchez JL, Dierig DA, Diaz Solis H, de la Rosa-Loera A** (2007) *Lesquerella fendleri* response to different sowing dates in northern Mexico. *Industrial Crops and Products* **25**, 117-122
- Roetheli JC, Carlson KD, Kleiman R, Thompson AE, Dierig DA, Glaser LK, Blase MG, Goodel J** (1991) *Lesquerella* as a source of hydroxy fatty acids for industrial products. Growing industrial material series. USDA/CSRS, Washington, DC
- Rollins RC, Shaw EA** (1973) *The Genus Lesquerella (Cruciferae) in North America*, Harvard University Press, Cambridge, Massachusetts, 288 pp
- Suneson CA, El Sharkawy A, Hall WE** (1963) Progress in 25 years of perennial wheat development. *Crop Science* **3**, 437-438
- Thompson AE, Dierig DA** (1994) Initial selection and breeding of *Lesquerella fendleri*, a new industrial oilseed. *Industrial Crops and Products* **2**, 91-106
- Tsitsin NV** (1965) Remote hybridization as a method of creating new species and varieties of plants. *Euphytica* **14**, 326-330
- Vega CRC, Sadras VO, Andrade FH, Uhart SA** (2000) Reproductive allometry in soybean, maize and sunflower. *Annals of Botany* **85**, 461-468
- Wagoner P** (1990) Perennial grain development: Past efforts and potential for the future. *Critical Reviews in Plant Sciences* **9**, 381-408
- Watson MA** (1984) Developmental constraints: Effect on population growth and patterns of resource allocation in a clonal plant. *The American Naturalist* **123**, 411-426
- Windauer L** (2002) Puesta en cultivo de especies del género *Lesquerella*: Influencia de factores ambientales sobre el desarrollo. MSc thesis, Escuela para Graduados de la Facultad de Agronomía, Universidad de Buenos Aires, Argentina, 118 pp
- Windauer L, Slafer GA, Ravetta D** (2004) Phenological responses to temperature of an annual and a perennial *Lesquerella* species. *Annals of Botany* **94**, 139-144
- Windauer L, Slafer GA, Ravetta D, Benech-Arnold RL** (2006) Environmental control of phenological development in two *Lesquerella* species. *Field Crops Research* **96**, 320-327
- Windauer L, Altuna A, Benech-Arnold R** (2007) Hydrotime analysis of *Lesquerella fendleri* seed germination responses to priming treatments. *Industrial Crops and Products* **25**, 70-74