industrial crops and products 27 (2008) 249–256

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Biomass allocation patterns and reproductive output of four *Oenothera* L. accessions native to Argentina

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ARTICLE INFO

Article history:
Received 10 August 2007
Received in revised form
17 September 2007
Accepted 27 September 2007

Keywords:
New crops
Evening primrose
γ-linolenic acid
Reproductive effort
Path analysis

ABSTRACT

Evening primrose (*Oenothera* spp.) has the potential to become an alternative oilseed crop in Patagonia, Argentina. This paper describes and compares phenology and allocation patterns of four wild accessions of *Oenothera* grown in a common garden, under non-limiting conditions. Our objective was to identify useful traits to shorten the domestication process. Accessions differed in the duration of the vegetative growth phase, which was negatively correlated to seed production per plant (reproductive output). Fruit set ranged between 70% and 95%, and did not differ among accessions. Differences found in the rate of capsule production did not explain the observed disparity in the number of fruits per plant. Reproductive output was mainly affected by the number of fruits per plant, vegetative biomass, and the proportion between seeds and total biomass (reproductive effort). Individual seed mass did not affect total seed production per plant. Seed-oil content was similar to that of domesticated species of evening primrose, but the content of gamma-linolenic acid was far too low (<2%) in comparison to the minimum acceptable standard necessary for seed commercialization (9%). *Oenothera* wild accessions are prone to seed losses by shattering. We concluded that short vegetative growth phase and high vegetative biomass would be useful traits for selection in breeding programs. Fruit shattering and low gamma-linolenic acid content are the main drawbacks that should be overcome to facilitate the domestication of one of these wild accessions.

1. Introduction

Oenothera L. (evening primrose) is a relatively new, high-value oilseed crop for temperate regions. Seeds contain 17–25% oil, which is an important commercial source of γ-linolenic acid (GLA), an essential fatty acid with proven applications as a nutrient and pharmaceutical for humans (Fieldsend and Morison, 2000a). The production of evening primrose has been established in northern and eastern Europe, North America and Australasia (Simpson and Fieldsend, 1993), and has been suggested as a new seed-oil crop suitable for Patagonia, Argentina (Ravetta and Soriano, 1998). Thirty native species of *Oenothera* have been described in Argentina (Munz, 1933; Dietrich, 1977; Hoch, 1988) and have yet to be evaluated for yield potential.

The morphological and phenological traits selected for an oil-seed crop usually consist in plants with (i) a determinate growth habit, required for uniform ripening of fruits (Çagirgan, 2006; Ghasemnezhad and Hornermeier, 2007); (ii) an adequate duration of the vegetative growth phase for the targeted environment (Habekotté, 1997; Ploschuk et al., 2003); (iii) a high rate of flower and fruit production; (iv) indehiscent fruits (Pascual-

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doi:10.1016/j.indcrop.2007.09.005

Villalobos et al., 1994); (v) a high number of fruits per plant (Asare and Scarisbrick, 1995); (vi) a high proportion of the economically useful part of the plant (Adamsen et al., 2003; Dingkuhn et al., 2006; Giunta et al., 2007); (vii) high oil and target fatty-acid content (Fieldsend and Morison, 2000a).

Here, we describe and compare the duration of vegetative growth phase, allocation patterns, seed-oil content and fatty-acid composition of individual plants of four accessions of *Oenothera* grown in a common garden in Patagonia, Argentina. Our purpose was to determine the relative importance of these traits for the selection of improved accessions of currently wild evening primrose.

We performed a path analysis in order to unravel the comparative contribution of these traits to reproductive output. We considered three attributes: fruit number per plant, seed number per fruit and seed mass. Fruit number was further analyzed as a function of the rate of production and duration of the vegetative phase. The utility of these traits for breeding programs is discussed.

2. Material and methods

2.1. Plant material

We evaluated two species, *Oenothera mendocinensis* Gillies ex Hooker et Arnott and *Oenothera odorata* Jacquin, sympatric in the Monte Desert. *O. odorata* is widely distributed in Patagonia, from Neuquén to Santa Cruz. Bulk seeds were collected from Las Leñas, Mendoza (ID 753, 35°11′729″S, 69°47′396″W, 1828 m a.s.l.) Since *O. mendocinensis* is a common species in Western Argentina, spread from 33°S to 46°S, and plant adaptive strategies to the stresses normally encountered by different populations may differ concomitantly with environmental differences over their distribution range (Berger et al., 2002), two populations were evaluated in our study: one native to the north-west of the area (hereafter referred to as *O. mendocinensis* N, ID 738 located in 33°03′158″S, 69°17′201″W, Tupungato, Mendoza, 2318 m a.s.l.) and one native to the south-west of the country (hereafter referred to as *O. mendocinensis* S, ID 863 located in 46°26′910″S, 70° 12′ 781″W, El Pluma, Santa Cruz, 464 m a.s.l.). A natural occurring hybrid (*O. odorata* × *O. mendocinensis*, hereafter referred to as "hybrid"; ID 756, located in 35°08′773″S, 70°04′690″W, Las Leñas, Mendoza, 2256 m a.s.l.) was also included in this study.

2.2. Study site and experimental conditions

The four accessions of *Oenothera* described above were grown in a common garden, in Gaiman, Chubut, Argentina (43°21′31″S; 65°38′39″W). The common garden approach has the advantage of making studies with populations from different regions possible, and it also limits variation due to heterogeneity of environmental conditions (Becker et al., 2006). At the same time, conditions are more benign than in the native environment (roadsides and other eroded areas) to permit the expression of the reproductive potential of each genotype.

In the experimental area the mean annual precipitation is 179 mm, the mean low temperature of the coldest month (June and July) is 1 °C and the absolute minimum air temperature is −10.8 °C.

At the beginning of February 2004, seeds were sown in germination trays filled with soil, peat moss and sand in equal proportion and maintained in a greenhouse, where they received 80% of outside light levels and temperature ranged between 25 and 15 °C (average maximum daytime and average minimum nighttime temperature). Seedlings were transplanted to the field 45 days after sowing (April 2004). Experimental units within this common garden consisted in plots of 150 individual plants (4 reps per accession for a total of 600 plants per accession). Accessions were randomly assigned to each plot. Plant density was 21 plants m^{-2} (30 cm between rows, 15 cm between plants). Density was low enough to avoid intraspecific competition and detrimental effects on final individual biomass and reproductive output (Kromer and Gross, 1987). Plants were flood irrigated every 15 days. Weed control was done by hand-pulling.

2.3. Vegetative and reproductive variables

Plants were considered to be in vegetative growth phase from the time of seeding to the day in which at least 50% of the individuals in each plot showed at least one flower in anthesis. Fruit set was determined in five flowers per plant (10 plants/plot; 4 plots/accession). The rate of capsule production (RCP) was calculated from bolting to the date of final harvest (5 plants/plot; 4 plots/accession). The final number of capsules per plant (5 plants/plot; 4 plots/accession), the number of seeds per capsule and seed weight (5 reps/plant; 5 plants/plot; 4 plots/accessions) were recorded 349 days after sowing. Reproductive output and reproductive effort (RE) were calculated, like measures of reproductive allocation of individual plants (5 plants/plot; 4 plots/accessions), as follows:

- Reproductive output = number of seeds per fruit *x* individual seed weight × number of fruits per plant.
- Reproductive effort = seed biomass/total biomass (Reekie and Bazzaz, 1987).

Mean values obtained from 100 individual observations (5 fruits/plant, 5 plants/plot; 4 plots/accessions), were used for the calculations of RE and reproductive output.

Fruit shattering was recorded 285, 293, 306, 318 and 336 days after sowing. The total number of flowers and the number of shattered and non-shattered fruits per plant were recorded in each date (5 plants/plot; 4 plots/accessions).

Plants were harvested (3 plants/plot; 4 plots/accession), 371 days after seeding. Leaves, stems and roots were separated and placed in an oven at 60 °C and weighed daily until constancy.

2.4. Chemical analyses

Seed-oil content was determined by Soxhlet extraction. Seed samples were oven-dried overnight at 80 °C and then allowed to cool in a desiccator. Samples (1–3 g) were ground to a fine meal and extracted with hexane for 5 h (IUPAC Method 1.122). The fatty-acid composition of the oil was determined by gas–liquid chromatography of fatty-acid methyl esters.

The fatty-acid methyl esters were obtained by transesterification with cold methanolic solution of potassium hydroxide (Christie, 1999). Oil samples (0.1 g) were diluted in 2 mL of hexane and 0.2 mL of 2N methanolic hydroxide solution was added. After stratification, 1 μL from the upper layer, containing the methyl esters, was injected into a Hewlett-Packard 5890 gas chromatograph (Hewlett-Packard, Sacramento, CA) equipped with a flame ionization detector and a CP-Wax 52 CB (Chrompack, Holland) capillary column (25 m length; 0.32 mm i.d.; 0.22 μm film thickness) of fused silica. Nitrogen was used as carrier gas, and the injector and detector temperatures were 250 and 260 °C. Oven temperature was programmed at 180 °C for 5 min, then 180–240 °C at 4 °C min^{-1}, then 240 °C for 10 min. The fatty acids were identified by comparison with retention times of a known standard mixture (AOCS-1, Sigma–Aldrich, St. Louis, MO).

2.5. *Statistical analyses*

Phenological and morphological variables were analyzed using one-way ANOVA, with accession (four levels) as the factor. To determine whether variables were adequately modeled by a normal distribution, the Shapiro–Wilks test was used. To check for variance homogeneity, the Cochran's *C* test was used. Comparison of means among accessions was assessed by Tukey's test. All analyses were done using Statgraphics 5.0 (Statistical Graphics Corp.). Fruit shattering was analyzed using a repeated measures ANOVA design. To gain more insight into the relative contribution to reproductive output of phenological and allocation patterns, a path analysis was performed, using the program package AMOS (Arbuckle and Wothke, 1999).

3. Results

3.1. *Phenology and allocation patterns*

All evening primrose accessions were transplanted to the field during early autumn and survived as an acaulescent rosette during winter. Eighty percent of the seedlings tolerated freezing temperatures (data not shown) and no differences were found in winter survival among accessions ($P = 0.84$). Plants remained in a vegetative state for 7–9 months. The duration of this vegetative growth phase differed among accessions: *O. mendocinensis* N was the first and *O. odorata* the last accession to bloom (Table 1). Standard error is zero (Table 1) because for every accession, the day in which at least one flower was opened was the same for the four plots. Therefore, it was not possible to estimate the mean square error of the variable and analysis of variance could not be conducted. Fruit set ranged between 70% and 95% and did not differ among accessions (Table 1). The rate of capsule production (RCP) was significantly lower in *O. mendocinensis* S than in the other three accessions, among which no differences were found (Table 1).

O. mendocinensis N showed a significantly higher number of fruits per plant than *O. mendocinensis* S and *O. odorata*, at harvest time (371 days after seeding; Table 1). The hybrid accession showed a higher number of seeds per fruit than the other accessions (Table 1) but this variable was not related

Table 1 – Results of the one-way ANOVA for comparison of phenological and morphological attributes of four *Oenothera* accessions native to Argentina, grown in a common garden in the Chubut River Valley factor is accession with four levels[a]

	d.f. error	*F*	*P*	*Oenothera odorata*	*Oenothera mendocinensis* N	*Oenothera mendocinensis* S	Hybrid
Vegetative growth phase (days)[b]				272 ± 0	232 ± 0	246 ± 0	246 ± 0
Fruit set	12	2.46	0.12	0.8 ± 0.10 a	0.9 ± 0.01 a	0.7 ± 0.01 a	0.95 ± 0.07 a
RCP (capsule day^{-1})[c]	12	4.73	0.015	0.73 ± 0.06 b	0.80 ± 0.06 b	0.49 ± 0.06 a	0.71 ± 0.06 b
Fruits per plant (*n*)	12	5.01	0.019	20.8 ± 3.3 a	54.8 ± 4.3 c	26.4 ± 12.5 ab	44.2 ± 11.5 bc
Seeds per capsule (*n*)	12	19.01	0.001	159.2 ± 20.1 ab	142.3 ± 20.5 a	207.1 ± 8.0 b	265.8 ± 10.9 c
100 seed mass (g)	12	1.02	0.42	0.027 ± 0.002 a	0.024 ± 0.002 a	0.024 ± 0.002 a	0.022 ± 0.002 a
Reproductive output (g pl^{-1})	12	2.22	0.143	1.04 ± 0.20 a	1.99 ± 0.38 a	1.42 ± 0.32 a	2.51 ± 0.65 a
Reproductive effort (g g^{-1})	12	5.81	0.013	0.10 ± 0.004 a	0.22 ± 0.037 b	0.13 ± 0.010 a	0.16 ± 0.007 a
Vegetative biomass (g)	12	8.7	0.003	3.97 ± 0.45 b	0.92 ± 0.07 a	4.57 ± 0.99 b	2.88 ± 0.55 b

[a] Data is mean ± S.E. Different letters within a row indicate significant differences among accessions ($P < 0.05$). Comparison of means among accessions was assessed by Tukey's test.
[b] It was not possible to estimate the mean squares error of the vegetative growth phase and thus, analysis of variance could not be conducted.
[c] RCP = rate of capsule production.

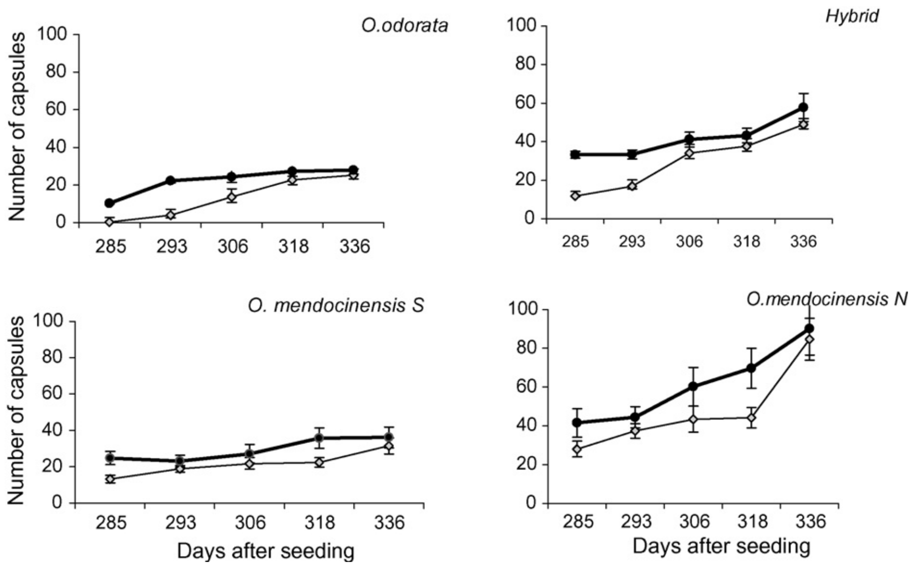

Fig. 1 – Fruit shattering in four wild accessions of *Oenothera*, grown in a common garden in the Chubut River Valley. The total number of capsules (closed signs) and the number of dehiscent capsules (open signs) per plant were recorded between 285 and 336 days after sowing. Each point represents the mean value of four plots ±S.E.

($P > 0.05$; R^2: 0.14) to seed production per plant (reproductive output). Individual seed mass did not differ among accessions and did not have a significant effect on reproductive output ($P > 0.05$; R^2: 0.003).

The proportion of biomass allocated to the economically useful part of the plant (reproductive effort) varied between 0.1 and 0.2 (Table 1). *O. mendocinensis* showed a higher reproductive effort that the other accessions (Table 1).

The genus *Oenothera* is prone to seed losses by shattering. *O. odorata* and *O. mendocinensis* (N and S) capsules shattered as soon as they ripened, while the hybrid accession showed the lowest fruit shattering during mid-Spring (days 285–300 in Fig. 1).

3.2. *Seed-oil content and composition*

Whereas similar contents of seed-oil were found in every accession, chromatography revealed significant differences in fatty-acid composition (Table 2). *O. odorata* showed a significantly lower content of linoleic (18:2), the major component of the fatty-acid profile, as well as higher oleic (18:1) content (Table 2). Palmitic acid (16:0) was lower in *O. mendocinensis* (N and S; Table 2).

Gamma-linolenic acid (GLA) values ranged from 1.1% to 1.6%. *O. mendocinensis* S had a significant higher GLA content than the rest (Table 2). GLA content was not related to seed-oil content ($P > 0.05$; R^2: 0.02).

Table 2 – Seed-oil content and fatty-acid profile of four *Oenothera* accessions native to Argentina, grown in a common garden in the Chubut River Valley[a]

	d.f. error	F	P	O. odorata	O. mendocinensis N	O. mendocinensis S	Hybrid
Oil	12	2.43	0.12	22.6 ± 0.7 a	23.2 ± 0.2 a	17.6 ± 3.2 a	19.2 ± 1.1 a
Fatty acids[b]							
14:0	12	0.24	0.86	0.0 ± 0.1 a	0.0 ± 0.0 a	0.1 ± 0.0 a	0.1 ± 0.0 a
16:0	12	9.5	0.002	8.3 ± 0.1 b	7.7 ± 0.2 a	7.6 ± 0.1 a	8.3 ± 0.1 a
16:1	12	1.02	0.42	0.1 ± 0.0 a	0.1 ± 0.0 a	0.1 ± 0.0 a	0.1 ± 0.0 a
18:0	12	14.91	0.001	2.4 ± 0.0 a	2.6 ± 0.0 b	2.7 ± 0.0 b	2.6 ± 0.0 b
18:1	12	11.89	0.001	10.8 ± 0.3 b	9.4 ± 0.2 a	9.4 ± 0.1 a	9.4 ± 0.2 a
18:2	12	8.06	0.003	76.7 ± 0.4 a	78.4 ± 0.1 b	78.0 ± 0.2 b	77.9 ± 0.2 b
18:3a	12	5.18	0.02	1.1 ± 0.1 a	1.1 ± 0.0 a	1.6 ± 0.1 b	1.2 ± 0.1 ab
18:3b	12	0.06	0.98	0.2 ± 0.0 a	0.2 ± 0.0 a	0.2 ± 0.0 a	0.2 ± 0.0 a
20:0	12	7	0.01	0.2 ± 0.0 a	0.2 ± 0.0 a	0.2 ± 0.0 a	0.2 ± 0.0 a
20:1	12	1.08	0.39	0.1 ± 0.0 a	0.1 ± 0.0 a	0.1 ± 0.0 a	0.1 ± 0.0 a

[a] Seed-oil content is presented as percentage on seed dry weight basis. Fatty-acid profile is presented as percentages of total seed-oil content. Values are means ($n = 4$). Means followed by different letters within a row are significantly different ($P < 0.05$).

[b] 14:0 = miristic acid, 16:0 = palmitic acid, 16:1 = palmitoleic acid, 18:0 = stearic acid, 18:1 = oleic acid, 18:2 = linoleic acid, 18:3a = gamma-linolenic acid, 18:3b = alpha-linolenic acid, 20:0 = arachidic acid, 20:1 = arachidonic acid.

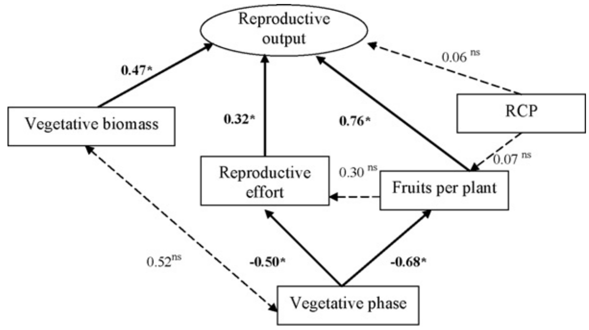

Fig. 2 – Path diagram showing the effects of phenology and plant attributes on reproductive output. RCP = rate of capsule production. Numbers indicate direct β path coefficients between traits. Asterisks indicate significance of the coefficient ($P < 0.05$). Total and indirect effects are listed in Table 3.

Table 3 – Total and indirect path coefficients (β), calculated by using a path analysis, of the effects of vegetative biomass, rate of capsule production (RCP), duration of vegetative phase, number of fruits per plant (No. fruits) and reproductive effort (RE) on reproductive output (RO) and No. fruits (see Fig. 2)

	Total effects					Indirect effects				
	Vegetative biomass	RCP	Vegetative phase	No. fruits	RE	Vegetative biomass	RCP	Vegetative phase	No. fruits	RE
No. fruits	0.00	0.07	**−0.68**	0.00	0.00	0.00	0.00	0.00	0.00	0.00
RE	0.00	0.02	**−0.70**	0.30	0.00	0.00	0.00	0.00	0.00	0.00
RO	**0.47**	0.11	**−0.74**	**0.85**	**0.32**	0.00	0.06	−0.74	0.10	0.00

Bold numbers indicate significant coefficients ($P < 0.05$). Direct path coefficients are indicated in Fig. 2.

3.3. *Relative contribution of attributes to reproductive output*

Reproductive output was affected positively by the number of fruits per plant, reproductive effort and vegetative biomass (Fig. 2) and negatively by the duration of the vegetative phase (Table 3). The relative total effect of the number of fruits per plant on reproductive output was higher than that of vegetative biomass or reproductive effort, as indicated by the higher path coefficients (β; Table 3).

The duration of the vegetative growth phase had a direct effect on the number of fruits per plant and reproductive effort (Fig. 2). Indirectly, it also affected reproductive output, through a negative effect on reproductive effort and on the number of fruits per plant. Its total negative effect was greater on reproductive output than on the other two variables (Table 3). RCP did not explain differences found in the total number of fruits per plant or reproductive output (Fig. 2; Table 3). Reproductive effort was not affected, as expected, by the number of fruits per plant (Fig. 2).

4. Discussion

Currently, many wild species are coming under considerable scrutiny in breeding and germplasm evaluation programs around the world, because of the necessity to diversify cropping systems (Berger et al., 2002; Dingkuhn et al., 2006).

The first steps of domestication require some knowledge of reproductive, vegetative and genetic variation of wild populations of the potential candidates (García et al., 1997; Ravetta and Soriano, 1998; Wendel and Cronn, 2003).

All *Oenothera* populations included in this experiment have an indeterminate growth habit, which prevents all seeds in a crop maturing at once. Furthermore, early harvesting of immature seeds can reduce yield quality and late harvesting can enhance fruit shattering. Capsule dehiscence is a major issue that should be overcome in order to accomplish a high reproductive output. Harvest management techniques have been proposed, as a way of limiting seed losses and improving seed quality in evening primrose (Ghasemnezhad and Hornermeier, 2007), but these methods require a plant variety bearing a certain number of matured non-shattering fruits during harvest time. In our experiment, the hybrid accession has the potential for higher seed-yields based on the relatively stable number of non-shattering fruits during nearly 12 days. Another option to avoid seed losses is the selection of non-shattering genotypes from spontaneous mutants from natural populations or induced through mutation breeding, as was it has been previously done for other new crops (Pascual-Villalobos et al., 1994).

Yield advances in traditional crops have come mainly through improvements in reproductive effort, an allocation measure similar to harvest index (Loomis and Connor, 1992). Reproductive effort is the proportion between the organs of economic significance and total biomass, therefore, small plants, such as those of wild accessions of *Oenothera*, despite having a similar reproductive effort than that of their domesticated relatives (Fieldsend and Morison, 2000a), yielded a reduced amount of seeds. Consequently, during the initial stages of the domestication process, selecting for higher individual plant biomass would be more effective than improving reproductive effort. Nevertheless, breeding for increased biomass should be done within the constrains imposed by environmental conditions of the targeted environment, avoiding the generation of a water-consuming crop (McLaughlin, 1985) and the ecological problems associated with excessive and, at times, inefficient irrigation in arid lands (Deng et al., 2006).

The number of fruits per plant had a major impact on the reproductive output of *Oenothera* (Fig. 2). Nonetheless, this variable does not seem to be useful for breeding programs, because heritability of this trait is usually low, since it is mainly governed by environmental conditions (Richards and Thurling, 1979) and competition (Diepenbrock, 2000). However, low heritability traits can be improved directly by crop management practices such as nitrogen application (Asare and Scarisbrick, 1995; Adamsen et al., 2003) or indirectly through selection of other high heritability traits, which have a significant effect on the former. In this regard, an early bolting demonstrated to be advantageous for *O. mendocinensis* N, resulting in the highest number of fruits per plant. Similar results were found in other crops, where the highest production of fruits was found in plants that flowered first and had the longest flowering period (Berger et al., 2002; Vignolio et al., 2002; Ploschuk et al., 2003). The factors influencing the timing of bolting in *Oenothera* comprise rosette size (Hirose and Kachi, 1982), vernalization and long-day photoperiod (Kachi and Hirose, 1983). The vegetative growth period is of great importance, because the life cycle of evening primrose in short-season areas such as Patagonia (Cabrera, 1994), is limited by the duration of the growing season, and an increase in the duration of the vegetative phase is followed by a concomitant decrease in the duration of the grain-filling period. Considering a fixed and common date for the end of the reproductive period, the number of fruits per plant mostly depends on early bolting. In theory, it also depends on fruit set and the rate of capsule production, but in our experiment the former was similar among the studied accessions and the latter had a non-significant effect on the final number of fruits. Therefore, the duration of the vegetative phase constitutes one of the key yield components. This variable has been used as a criterion for selection in breeding programs for several species, i.e. chickpea (Berger et al., 2006), wheat (Mahfoozi et al., 2006) and groundnut (Upadhyaya et al., 2006), to avoid drought or temperature stresses.

Seed-oil content ranged between 17% and 23% (Table 2). These values are similar to those described for wild and cultivated evening primrose (Wolf et al., 1983; Christie, 1999; Fieldsend and Morison, 2000b). The GLA content found in our accessions were upto 1.6%. These concentrations are similar to that found in some other species of the genus (Velasco and Goffman, 1999), but very low in comparison to the minimum acceptable standard for the nutritional supplements industry content (9%; Fieldsend and Morison, 2000b). Nevertheless, there are several options available to enhance GLA production. Possibilities range from the employment of genetic engineering protocols (Liu et al., 2001; Mendoza de Gyvest et al., 2004) to the application of relatively simple management techniques, i.e. breeding early cultivars (Levy et al., 1993) or harvesting in late Spring (Ghasemnezhad and Hornermeier, 2007). The cultivation of early cultivars can help increase the activity of Δ 6-desaturase. Several authors demonstrated that this enzyme is affected by heat (more than 27 °C) and that the occurrence of high temperatures during seed-filling (30–40 days after anthesis; Levy et al., 1993) is the main cause for the low GLA content (Yaniv et al., 1989; Fieldsend and Morison, 2000b).

Our results indicate that there was no significant relationship between seed-oil content and GLA content (Table 2). Similar results were found by Fieldsend and Morison (2000b) for *Oenothera biennis*. As these variables are not negatively associated, GLA content might be used as a selection criterion without restraining selection for seed-oil content.

5. Conclusions

Four accessions of evening primrose native to Argentina were evaluated for their potential as crops. The influence of phenological and allocation patterns on reproductive output were analyzed with the purpose of proposing criteria for breeding programs. We concluded that the following traits would provide useful selection criteria to improve reproductive output and seed quality: (1) a short vegetative phase (early bolting) would be advantageous in terms of prolonging the reproductive season and enhancing GLA content; (2) plants with higher vegetative biomass; and (3) higher number of fruits per plant. Management practices such as fertilization should be tested in order to improve the last two traits. The main drawbacks that should be overcome to facilitate the domestication of one of these accessions are (1) fruit shattering and (2) low gamma-linolenic content.

On the basis of phenological and allocation patterns, the hybrid accession is the best candidate to become a new crop. *O. mendocinensis* and *O. odorata* have little to offer, on the basis of very poor agronomy, including a low reproductive effort, tendency to shatter, and late bolting.

Acknowledgements

This work was funded by Agencia Nacional de Promoción Científica y Tecnológica (PID 009 and PID 363) and Ministerio de la Producción de la Provincia del Chubut, Argentina.

REFERENCES

Adamsen, F.J., Coffelt, T.A., Nelson, J.M., 2003. Flowering and seed yield of *Lesquerella* as affected by nitrogen fertilization and seeding rate. Ind. Crops Prod. 18, 125–231.

Arbuckle, J.L., Wothke, W., 1999. AMOS 4.0 User's Guide. SPSS, SmallWalters, Chicago.

Asare, E., Scarisbrick, D.H., 1995. Rate of nitrogen and sulphur fertilizers on yield, yield components and seed quality of oilseed rape (*Brassica napus* L.). Field Crops Res. 44, 41–46.

Becker, U., Reinhold, T., Matthies, D., 2006. Effects of pollination distance on reproduction and offspring performance in *Hypochoeris radicata*: experiments with plants from three European regions. Biol. Conserv. 132, 109–118.

Berger, J., Robertson, L., Cocks, P., 2002. Agricultural potential of Mediterranean grain and forage legumes: key differences between and within *Vicia* species in terms of phenology, yield, and agronomy give insight into plant adaptation to semi-arid environments. Genet. Resour. Crop Evol. 49, 313–325.

Berger, J., Ali, M., Basu, P., Chaudhary, B., Chaturvedi, P., Deshmukh, P., Dharmaraj, P., Dwivedi, S., Gangadhar, G., Gaur, P., Kumar, J., Pannu, R., Siddique, K., Singh, D.N., Singh, D.P., Singh, S., Turner, N., Yadava, H., Yadav, S., 2006. Genotype by environment studies demonstrates the critical role of phenology in adaptation of chickpea (*Cicer arietinum* L.) to high and low yielding environments of India. Field Crops Res. 98, 230–244.

Cabrera, A., 1994. Regiones fitogeográficas Argentinas. Enciclopedia Argentina de Agricultura y Jardinería. Tomo II, Fascículo 1. Acme S.A.C.I, pp. 85.

Çagirgan, M.I., 2006. Selection and morphological characterization of induced determinate mutants in sesame. Field Crops Res. 96, 19–24.

Christie, W.W., 1999. The analysis of evening primrose oil. Ind. Crops Prod. 10, 73–83.

Deng, X., Shan, L., Zhang, H., Turner, N.C., 2006. Improving agricultural water use efficiency in arid and semiarid areas of China. Agric. Water Manage. 80, 23–40.

Diepenbrock, W., 2000. Yield analysis of winter oilseed rape (*Brassica napus* L.): a review. Field Crops Res. 67, 35–49.

Dietrich, W., 1977. The South American species of *Oenothera sect. Oenothera* (Raimannia, Renneria, Onagraceae). Ann Missouri Bot. Gard. 64, 425–626.

Dingkuhn, M., Singh, B.B., Clerget, B., Chantereau, J., Sultan, B., 2006. Past, present and future criteria to breed crops for water-limited environments in West Africa. Agric. Water Manage. 80, 241–261.

Fieldsend, A.F., Morison, J.J.L., 2000a. Contrasting growth and dry matter partitioning in winter and spring evening primrose crops (*Oenothera* spp.). Field Crops Res. 68, 9–20.

Fieldsend, A.F., Morison, J.J.L., 2000b. Climatic conditions during seed growth significantly influence oil content and quality in winter and spring evening primrose crops (*Oenothera* spp.). Ind. Crops Prod. 12, 137–147.

García, E.H., Peña-Valdivia, C.B., Aguirre, J.R.R., Muruaga, J.S.M., 1997. Morphological and agronomic traits of a wild population and an improved cultivar of common bean (*Phaseolus vulgaris* L.). Ann. Bot. 79, 207–213.

Ghasemnezhad, A., Hornermeier, B., 2007. Seed yield, oil content and fatty-acid composition of *Oenothera biennis* L. affected by harvest date and harvest method. Ind. Crops Prod. 25, 271–274.

Giunta, F., Motzo, R., Pruneddu, G., 2007. Trends since 1900 in the yield potential of Italian-bred durum wheat cultivars. Eur. J. Agron. 27, 12–24.

Habekotté, B., 1997. Options for increasing seed yield of winter oilseed rape (*Brassica napus* L.): a simulation study. Field Crops Res. 54, 137–151.

Hirose, T., Kachi, N., 1982. Critical size for flowering in biennials with special reference to their distribution in a sand dune system. Oecologia 55, 281–284.

Hoch, P.C., 1988. Onagraceae, In: Correa M. Ed., Flora Patagónica. Dicotyledones dialipétalas (Oxalidáceae a Cornácea), Tomo VIII, Part V. Colección científica del INTA, Buenos Aires, pp. 288–298.

Kachi, N., Hirose, T., 1983. Bolting induction in *Oenothera erythrosepala* Borbás in relation to rosette size, vernalization, and photoperiod. Oecologia 60, 6–9.

Kromer, M., Gross, K., 1987. Seed mass, genotype, and density effects on growth and yield of *Oenothera biennis* L. Oecologia 73, 207–212.

Levy, A., Palevitch, D., Ranen, C., 1993. Increasing gamma-linolenic acid in evening primrose grown under hot temperatures by breeding early cultivars. Acta Hortic. 330, 219–225.

Liu, J., DeMichele, S., Bergana, M., Bobik, E., Hastilow, C., Chuang, L., Mukerji, P., Huang, Y., 2001. Characterization of oil exhibiting high gamma-linolenic acid from a genetically transformed canola strain. J. Am. Oil Chem. Soc. 78, 489–493.

Loomis, R.S., Connor, D.J., 1992. Crop ecology. In: Productivity and Management in Agricultural Systems. Cambridge University Press, New York, p. 538.

Mahfoozi, S., Limin, A.E., Ahakpaz, F., Fowler, D.B., 2006. Phenological development and expression of freezing resistence in spring and winter wheat under field conditions in north-west Iran. Field Crops Res. 97, 182–187.

McLaughlin, S.P., 1985. Economic prospects for new crops in the southwestern United States. Econ. Bot. 39, 473–481.

Mendoza de Gyvest, E., Sparks, C., Sayanova, O., Lazzeri, P., Napier, J., Jones, Huw., 2004. Genetic manipulation of γ-linolenic acid (GLA) síntesis in a comercial variety of evening primrose (*Oenothera* sp.). Plant Biotechnol. J. 2, 351–357.

Munz, P.A., 1933. Las Onagráceas de la Argentina. Physis 11, 266–292.

Pascual-Villalobos, M.J., Röbbelen, G., Correal, E., 1994. Production and evaluation of indehiscent mutant genotypes in *Euphorbia lagascae*. Ind. Crops Prod. 3, 129–143.

Ploschuk, E., Cerdeiras, G., Windauer, L., Dierig, D., Ravetta, D., 2003. Development of alternative Lesquerella species in Patagonia (Argentina): potential of *Lesquerella angustifolia*. Ind. Crops Prod. 18, 1–6.

Ravetta, D., Soriano, A., 1998. Alternatives for the development of new industrial crops for Patagonia. Ecol. Aust. 8, 297–307.

Reekie, E.G., Bazzaz, F.A., 1987. Reproductive effort in plants. 1. Carbon allocation to reproduction. Am. Nat. 129, 876–896.

Richards, R.A., Thurling, N., 1979. Genetic analysis of drought stress response in rapeseed (Brassica campestris and B. napus). II. Yield improvement and the application of selection indices. Euphytica 28, 169–177.

Simpson, M.J.A., Fieldsend, A.F., 1993. Evening primrose: harvest methods and timing. Acta Hortic. 331, 121–128.

Upadhyaya, H., Reddy, L., Gowda, C., Singh, S., 2006. Identification of diverse groundnut germoplasm: sources of early maturity

in a core collection. Field Crops Res. 37, 261–271.
Velasco, L., Goffman, F.D., 1999. Tocopherol and fatty-acid composition of twenty-five species of Onagraceae Juss. Bot. J. Linn. Soc. 129, 359–366.
Vignolio, O., Fernández, O., Maceira, N., 2002. Biomass allocation to vegetative and reproductive organs in *Lotus glaber* and *L. corniculatus* (Fabaceae). Aust. J. Bot. 50, 75–82.
Wendel, J.F., Cronn, R.C., 2003. Polyploidy and the evolutionary history of cotton. Adv. Agron. 78, 139–186.
Wolf, R.B., Kleiman, R., England, R.E., 1983. New sources of gamma-linolenic acid. J. Am. Oil Chem. Soc. 60, 1858–1860.
Yaniv, Z., Ranen, C., Levy, A., Palevithc, D., 1989. Effect of temperature on the fatty-acid composition and yield of evening primrose (*Oenothera lamarckiana*) seeds. J. Exp. Bot. 40, 609–613.