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Short communication

Critical size for reproduction and ontogenetic changes in the allocation patterns of wild and domesticated species of evening primrose (*Oenothera* L.)

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ABSTRACT

Oenothera L. (evening primrose) has been suggested as a new seed-oil crop, source of gamma-linolenic acid, with uses herbal medicine industries. We compared the critical size for reproduction and the biomass allocation patterns during three phenological stages of a wild (*O. mendoncinensis*) and a domesticated species (*O.biennis*). Rosettes of *O. biennis* attained a critical size after two years in the field, while the wild species reproduced during the first year. Early bolting is a comprehensive strategy for indeterminate species growing in a short season environment, because it extends the flowering period but at the same time, the short vegetative period limits carbohydrates stores available for reproductive growth, and therefore, yield. Reproductive effort caused in both species a significant depletion of reserves during the flowering. Leaves and roots biomass declined by senescence after bolting in the wild species. In conclusion, yield improvement of wild species of *Oenothera* could be obtained by selecting plants with higher accumulation of vegetative biomass and delayed senescence that guarantees greater photosynthetic capacity after flowering.

1. Introduction

Oenothera L. (evening primrose) has been suggested as a new seed-oil crop suitable for Patagonia, Argentina (Ravetta and Soriano, 1998) since it contains gamma-linolenic acid (GLA), an essential fatty acid with proven uses in the pharmaceutical industry. Beneficial effects of GLA have been reported in rheumatic and arthritic conditions, atopic dermatitis, psoriasis, premenstrual and menopausal syndrome, and diabetic neuropathy (Mahady et al., 2001; Horrobin, 1990). Although other plant species such as borage (*Borago officinalis* L.) or blackcurrant (*Ribes nigrum* L.) offer higher GLA concentrations, evening primrose remains the most suitable source of GLA because of its very simple oil profile and its potential for agricultural production (Lapinskas, 1999; Liu et al., 2003; Ghasemnezhad, 2007). An increasing market for evening primrose seed has given farmers an opportunity to diversify into non-food production in northern and Eastern Europe, North America and Australasia (Simpson and Fieldsend, 1993). Rosette plants like *Oenothera* grow until they reach a critical size for reproduction. This mechanism, related to the accumulation of carbohydrates would ensure that individuals build up sufficient resources for a successful reproduction (Reekie, 1997). Thus, the size of an individual and the content of carbohydrate reserves at the end of the vegetative growth phase might be good predictors of seed output (Werner, 1975) and are more important than its chronological age in determining whether it remains vegetative, blooms or dies, (Kachi and Hirose, 1983). The pattern of biomass allocation is a central issue in plant life history (Müller et al., 2000). One of the most prominent commitments of life story is one that involves the cost of reproduction, manifested as decreased survival, vegetative growth or the potential for future reproduction (Reekie and Bazzaz, 1992). The high cost of reproductive structures decreases carbohydrate reserves (Chapin et al., 1990) increasing the risk of mortality (Snow and Whigham, 1989). Our objectives were (1) To compare the critical size for reproduction of a wild species native to low-resource environments (*O. mendocinensis*) and a domesticated species selected in for high-yield in high-resource environments (*O. biennis*). (2) To compare the allocation patterns of these species during three phenological stages. (3)To identify key traits associated with reproduction (yield and reproductive effort).

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2. Material and methods

We perform a field experiment with a wild and a domesticated species of *Oenothera* (*O. mendocinensis* and *O. biennis*, respectively). The seed-oil content and fatty acids profile of these species have been previously reported (Vilela et al., 2008; Christie, 1999; Ghasemnezhad and Honermeier, 2007; Sekeroglu and Ozguven, 2006). These species were grown in the Chubut River Valley, Patagonia Argentina (43°21′31″S; 65°38′39″W), where the mean annual precipitation is 179 mm. Fall (March) seeding was carried out in germination trays and transplanted in Spring (October), in a completely randomized design. Experimental units consisted in plots (8 plots per species; 35 plants per plot). Rows and plants were 0.15 m apart. Vegetative phase was calculated as the number of days from seeding to the day in which at least 50% of plants in each plot showed one flower in anthesis. Three plants per plot were harvested at three phenological phases (vegetative, flowering and fruit growth) and oven-dried at 60 °C until weight constancy. We calculated: (1) Leaf mass ratio (LMR; leaf biomass/total biomass; $g \times g^{-1}$); (2) root mass ratio (RMR; root biomass/total biomass;); (3) seed yield (g seed $\times$ pl^{-1}) = individual seed mass $\times$ number of seeds per fruit $\times$ number of fruits per plant; (4) reproductive effort (RE) = (fruit biomass + reproductive stems biomass)/total plant biomass ($g \times g^{-1}$; Thompson and Stewart, 1981); (5) TNC_{pool} = TNC concentration $\times$ root mass (g; Kobe et al., 2010) and (6) TNC mass ratio (TNCMR; TNC_{pool}/total biomass; $g \times g^{-1}$). Total non-structural carbohydrates concentration in root was determined by the Anthrone method (Yemm and Willis, 1954). Differences between species in biomass accumulation, allocation traits, root TNC content and seed yield as well as the effect of phenological stages on those traits were analyzed using two-way ANOVA. Means were compared using Tukeyís test. Rosette diameter was analyzed using *T*-test for independent samples. Relationships among traits were performed through linear regressions models. InfoStat 2009 was used for statistical analyses

3. Results

3.1. Critical size for reproduction

Rosettes of *O. biennis* larger than 17.34 ± 1.08 cm bolted and produced seeds. This critical size was attained by 13.05% of plants during the first year and 73.40% during the second year. Smaller rosettes remained vegetative after two years of experiment, with a mean diameter of 12.97 ± 0.42 cm. Every plant of *O. mendocinensis* attained the critical size of 18.87 ± 0.87 cm during the first year. The species did not differ in the critical size ($P = 0.29$; $T = -1.11$).

3.2. Allocation patterns

Vegetative phenophase: Rosettes of *O. biennis* showed higher total biomass and higher allocation to leaves (LMR) than those of *O. mendocinensis*, which showed preferential allocation to roots (RMR) and storage (TNCMR). Species did not differ in TNC_{pool} due to differences in biomass: larger plants of *O. biennis* with lower allocation to storage ended up with the same pool of carbohydrate reserves in roots than smaller plants of *O. mendocinensis* with higher TNCMR (Table 1). Root TNC concentration showed maximum values at the end of the vegetative stage (rosette, before bolting) and then decreased in both species throughout the reproductive cycle (Table 1). Flowering phenophase: From rosette to flowering, total plant biomass increased 40% in the wild species and 500% in *O. biennis*. Biomass increase in *O. biennis* was due to the production of reproductive structures, roots and leaves. Contrariwise, *O. mendocinensis* leaves and roots biomass declined by senescence and the increase of total biomass was only due to reproductive growth. The combination of vegetative biomass senescence and reproductive growth resulted in an extremely high RE for the wild species (63% of plant biomass; Table 1), higher than that of *O. biennis*. The significant decrease in TNC_{pool} indicates the use of carbohydrate reserves for flowering. Fruit growth phenophase: *O. mendocinensis* total biomass decreased by a 40% between flowering and fruiting phenophase while *O. biennis* continued growing throughout the reproductive cycle. Differences in number of fruits per plant and individual seed mass provoked a seed yield 8-fold higher in *O. biennis* than in *O. mendocinensis* (Table 1).

3.3. Traits association

Reproductive biomass was positively related to rosette diameter, to TNC_{pool} and vegetative biomass in *O. biennis* (Fig. 1A–C). In the wild species, reproductive biomass only resulted positively correlated with TNC_{pool} (Fig. 1B) and vegetative biomass during fruit phenology (Fig. 1D). Trade-offs between reproduction and storage (TNC_{pool}) and leaf biomass were found in *O. mendocinensis* (Fig. 2A and B). RE and leaf biomass was positively related in *O. biennis* (Fig. 2B).

Table 1
Biomass accumulation, partition and root carbohydrates storage in different phenological stages (rosette, flower and fruit) of two species of *Oenothera* growing in a common garden in the Chubut River Valley. Mean values ± S.E. are shown. Capital letters indicate differences between species for the same phenological stage, while small letters indicate differences between phenological stages for the same species ($P < 0.05$).

Variable	*O. mendocinensis*			*O. biennis*		
	Rosette	Flower	Fruit	Rosette	Flower	Fruit
Total biomass ($g \times pl^{-1}$)	1.49 ± 0.04 aA	2.09 ± 0.13 bA	1.80 ± 0.21 ab A	2.58 ± 0.23 aB	13.65 ± 1.13 bB	20.36 ± 2.91 bB
Leaf biomass ($g \times pl^{-1}$)	0.87 ± 0.03 cA	0.48 ± 0.05 bA	0.15 ± 0.03 aA	2.03 ± 0.20 aB	6.67 ± 0.42 bB	3.15 ± 0.54 aB
LMR	0.53 ± 0.06 cA	0.22 ± 0.02 bA	0.08 ± 0.01 aA	0.78 ± 0.01 cB	0.49 ± 0.02 bB	0.15 ± 0.02 aB
Root biomass ($g \times pl^{-1}$)	0.52 ± 0.03 bA	0.26 ± 0.01 aA	0.20 ± 0.03 aA	0.46 ± 0.05 aA	2.21 ± 0.20 bB	2.01 ± 0.32 bB
RMR	0.39 ± 0.05 bB	0.13 ± 0.01 aA	0.11 ± 0.005 aA	0.18 ± 0.01 bA	0.17 ± 0.01 bB	0.10 ± 0.01 aA
Reproductive biomass ($g \times pl^{-1}$)	–	1.31 ± 0.11 aA	1.44 ± 0.16 aA	–	4.49 ± 0.52 bB	15.01 ± 2.20 cB
RE	–	0.63 ± 0.02 aB	0.81 ± 0.01 bB	–	0.32 ± 0.01 bA	0.74 ± 0.02 cA
Vegetative biomass ($g \times pl^{-1}$)	1.49 ± 0.04 cA	0.75 ± 0.06 bA	0.35 ± 0.05 aA	2.58 ± 0.23 aB	8.88 ± 0.60 cB	5.16 ± 0.81 bB
TNCMR	0.07 ± 0.01 bB	0.02 ± 0.002 aA	0.01 ± 0.001 aA	0.04 ± 2.4E-3 cA	0.02 ± 0.001 bA	0.01 ± 0.0004 aA
TNC pool	0.10 ± 0.01 cA	0.03 ± 0.002 bA	0.02 ± 0.003 aA	0.09 ± 0.01 aA	0.29 ± 0.03 cB	0.19 ± 0.03 bB
Root TNC (%)	18.78 ± 0.69 cA	13.16 ± 0.39 bA	8.67 ± 1.02 aA	20.04 ± 0.67 cA	13.08 ± 0.41 bA	9.75 ± 0.37 aA
Seed yield (g seed $\times$ pl^{-1})	–	–	0.44 ± 0.05 A	–	–	3.57 ± 0.65 B
Fruits per plant (*n*)	–	–	10.04 ± 0.87 A	–	–	52.07 ± 8.89 B
Seeds per capsule (*n*)	–	–	174.41 ± 8.88 A	–	–	178.62 ± 7.07 A
Seed weight (g $\times$ 100 seed)	–	–	0.02 ± 0.001 A	–	–	0.04 ± 0.002 B

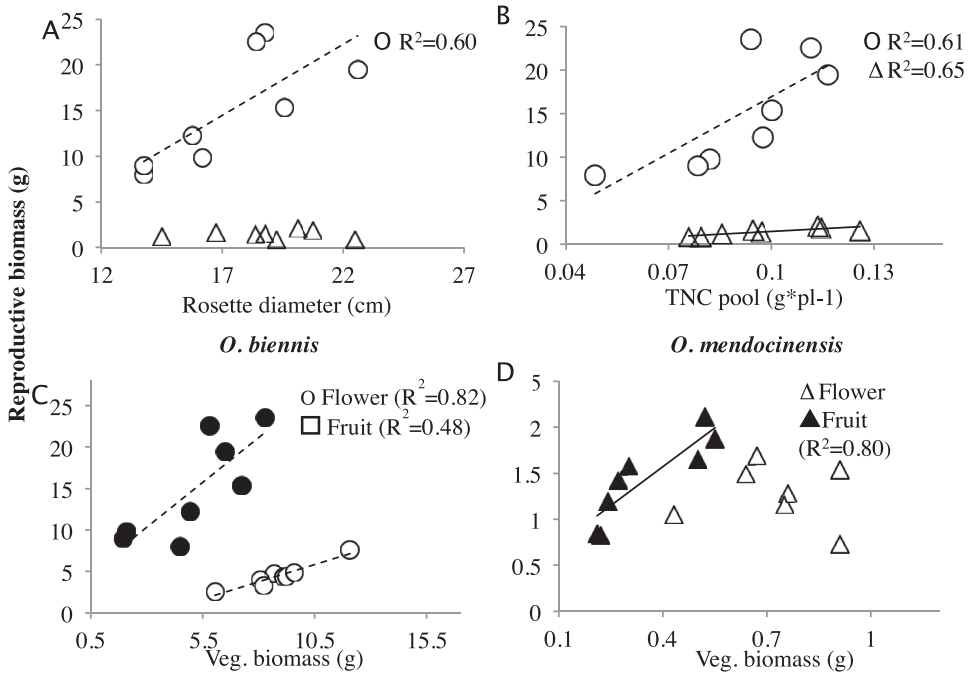

Fig. 1. Relationship between reproductive biomass and rosette diameter (A), rosette TNC pool (B) and vegetative biomass production during flowering and fruiting for *O. biennis* (O; C) and *O. mendocinensis* (Δ; D) growing in a common garden in the Chubut River Valley.

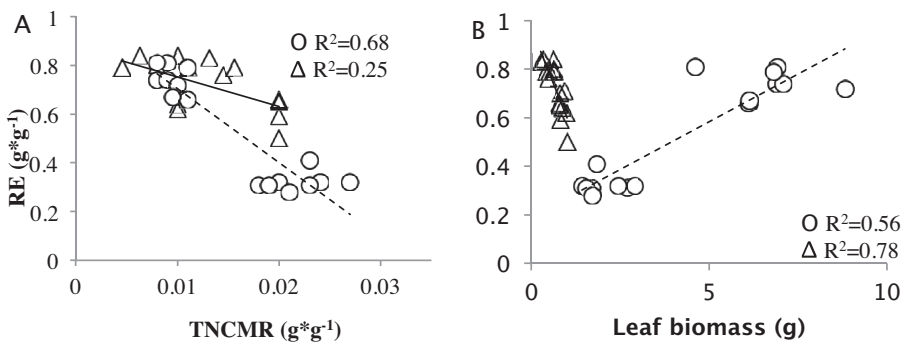

Fig. 2. Relationship between allocation to reproduction (RE), storage (TNCMR; A) and leaf biomass (B) of two species of *Oenothera* growing in a common garden in the Chubut River Valley. Solid lines and dashed lines represent the regression line calculated for *O. mendocinensis* (Δ) and *O. biennis* (O), respectively.

4. Discussion

Our results indicate that both species showed a similar critical size for reproduction but required different periods in the field to attain that size. The early bolting of *O. mendocinensis* might be a suitable strategy for a species growing in Patagonia, an area with short reproductive season because it extends the flowering period. On the other hand, the delayed reproductive strategy of *O. biennis* makes sense for a plant selected for high-yield because of the positive relationship found between rosette diameter, TNC_{pool} and reproductive biomass: larger plants with higher reserves produced higher yields than smaller plants. During the vegetative phase *O. mendocinensis* showed preferential allocation to functions that improve survivorship (Tilman, 1988) or reproduction (Chapin et al., 1990), such as storage (TNCMR) and storage organs (RMR) while *O. biennis* showed higher allocation to LMR. Since LMR is associated with greater RGR (Lambers et al., 1998), this allocation pattern resulted in rosettes of a similar diameter than *O. mendocinensis* but almost double total biomass. Sexual reproductive effort caused in both species a significant depletion of stored reserves, showed by the decrease of TNC% and TNCMR during flowering. Carbohydrates exhaustion stimulates tissues senescence, leading to the whole plant death (Munné-Bosch, 2008). This phenomenon is similar to that observed in annual crop plants, in which blooming induces the loss of the photosynthetic capacity of leaves (Pommel et al., 2006) and retraslocation of mineral nutrients to the fruits (Noodén, 1988). The process of senescence, when is induced prematurely as in *O. mendocinensis*, limits plant productivity through a decrease in the amount of biomass or yield (Gregersen et al., 2013). Nevertheless, the initial phase of senescence is reversible (Hörtensteiner and Feller, 2002) and the rate of senescence and remobilization of leaf nitrogen are related to the nitrogen nutrition status of the plant and on source:sink relations (Ono et al., 1999). In summary, the criteria for domestication of wild species of *Oenothera* should include (1) bigger vegetative plants because this might guarantee more carbohydrate stores available for reproductive growth; (2) delayed senescence of leaves and roots.

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