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Trade-offs between reproductive allocation and storage in species of *Oenothera* L. (Onagraceae) native to Argentina

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ABSTRACT

A trade-off between reproduction and survival arises because current reproduction diminishes levels of a limiting resource such that less can be placed in storage organs for the survival of an organism during the unfavorable season. *Oenothera* is a particularly suited genus for studying those kind of trade-offs because it contains species with different life-history strategies (annual, biennial and perennial). Since allocation to leaves is a major factor associated with changes in life-history, here we tested the hypothesis that *Oenothera* leaf attributes would affect plant reproductive effort and therefore, root reserves. We selected two groups of taxa differing in their leaf area ratio (low- and high-LAR) and we compared their pattern of resource allocation to growth, reproduction and storage. Path analysis confirmed our hypothesis that LAR is the most important variable in explaining variation in allocation to reproduction or storage. The group with high allocation to leaves assigned resources preferentially to storage while the other group allocated more resources to reproduction, as predicted. A trade-off between reproduction and storage was only confirmed for the high-LAR group. The low-LAR group showed the life-history tactic of annual plants, while the high-LAR group exhibited a strategy generally associated with perenniality.

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1. Introduction

Allocation theory assumes that organisms have a limited supply of a critical resource that they must divide among several competing functions, broadly defined as growth, maintenance, storage and reproduction (Bazzaz, 1997). These functions are further assumed to be mutually exclusive, consequently, increased allocation toward one function results in trade-offs with one or more competing functions. These detrimental changes in one trait linked to beneficial changes in another have played a central role in the development of a theory of life history evolution (Stearns, 1989). The most prominent

life-history trade-off involves the cost of reproduction, which may be manifested as a decrease in survival, vegetative growth or future reproduction (Biere, 1995; Huang et al., 2005; Lesica and Shelly, 1995; Reekie and Bazzaz, 1992; Worley and Harder, 1996). A trade-off between reproduction and survival arises because current reproduction exhausts a particular nutrient or the energy of an organism (Ehrlén and van Groenendael, 2001), thereby reducing its ability to invest in storage, which is essential for survival during the unfavorable season (Grime, 1979; Equiza et al., 1997).

Genera with taxa differing in life history are ideal for studying reproductive effort and trade-offs, because such

organisms are otherwise similar in many ways (Hautekeete et al., 2001). *Oenothera* L. (evening primrose; Onagraceae) is a particularly interesting system for evaluating potential trade-offs because there is evidence of life history evolution (monocarpy vs. polycarpy) and transitions between these annual, biennial and perennial strategies can be influenced by environmental conditions, such as winter temperature, season length or resource availability (Evans et al., 2005; Kachi and Hirose, 1983). There are 8 species of *Oenothera* native to southern Argentina (Patagonia), and although all of them have been described as annual or biennial (Munz, 1933; Hoch, 1988; Dietrich, 1977), our field observations, in accordance to Evans et al. (2005), indicate that most of these taxa produce seeds during the first year, survive after winter, and behave as iteroparous perennials. Since several studies indicate that allocation to leaves is a major factor associated with changes in growth and life history (Cornelissen et al., 1996; Poorter and Remkes, 1990; Reich et al., 1992), and, in particular for *Oenothera*, a critical leaf area might determine whether a species behaves as a winter annual or a biennial (Kachi and Hirose, 1983), we selected for this study two groups of taxa differing in their allocation to leaves, and we compared their pattern of resource allocation among growth, reproduction and storage.

Our objective was to determine whether *Oenothera* leaf attributes would affect plant reproductive effort and therefore, root reserves. Theoretical predictions indicate that allocation to leaves and biomass accumulation are positively correlated (Garnier, 1992; Veneklaas et al., 2002) and that vegetative growth is strongly coupled with reproductive allocation (Bazzaz, 1997; Klinkhamer et al., 1990, 1992; Hirose and Kachi, 1986). At the same time, under a trade-off there should be a negative correlation between growth and reserve storage (Chapin et al., 1990). Despite these predictions, our field observations lead us to the hypothesis that those taxa with high allocation to leaves will assign resources preferentially to growth and storage. Since the general consequence of allocating carbon to storage is a decrease in seed set (Chiariello and Roughgarden, 1984), we predict a concomitant reduction in reproductive effort.

Alternatively, we propose that those taxa with low allocation to leaves will assign more resources to reproduction than to growth or storage. This hypothesis is supported by studies that found that the elevated energy cost of reproductive tissues might draw down reserves (Chapin et al., 1990; Marquis et al., 1997; Cunningham, 1997) leading to an increased risk of mortality (Snow and Whigham, 1989). The relationship between size, reproduction and survival in *Oenothera*, has already been highlighted sufficiently by several authors (Kachi and Hirose, 1983,1985; Hirose and Kachi, 1982,1986). However, most studies focus on allocation to vegetative or reproductive functions, omitting storage as a possibility (Chiariello and Roughgarden, 1984).

Total biomass partition, leaf allocation (assessed as leaf area ratio), leaf morphology (assessed as specific leaf area), storage (assessed as root total non-structural carbohydrates) and reproductive effort were evaluated in order to test our hypotheses. We will focus on trade-offs -*sensu* Stearns, 1992- in which allocation decisions between two or more processes that compete directly with one another for limited resources

within a single individual are responsible for negative phenotypic correlations among life history traits.

2. Materials and methods

2.1. Study species and plant material

Oenothera species native to Patagonia are short-lived perennial herbs, up to 0.80 m height, commonly found in recently disturbed habitats. Leaves are alternate or basal. Flowers are yellow, red in age; hypanthium deciduous after flowering; sepals and petals four; stamens eight, equal or unequal; capsules straight, woody, four celled four valved dehiscent; seeds many, naked. As other *Oenothera* species, they exist as an acaulescent rosette in the vegetative state, and develop elongate stems bearing leaves, flowers and capsules in the reproductive state. For this experiment, we selected *Oenothera mendocinensis* Gilles ex Hooker et Arnott and *O. odorata* Jacquin, two species sympatric in the phytogeographical Monte region, in Argentina. Since *Oenothera mendocinensis* is widespread in Western Argentina, from 33°S to 46°S, and the specific genetic characteristics (self pollination and Renner's cycles; Dietrich, 1977) of the genus causes a high inter-population and low intra-population variability (Martínková et al., 2006), two populations were included in our study. Given that evening primrose possesses wide inter-specific fertility in sexual crosses that allows the exchange of chloroplasts and/or chromosome pairs between species by simple genetic crosses (Mráček et al., 2006), a crossbreed (*Oenothera odorata* × *O. mendocinensis* N, hereafter referred to as "hybrid"), was also included in this study. These four populations were chosen because they differ in their leaf allocation and several studies demonstrate that allocation to leaves is a major factor associated with changes in growth and life history.

Bulk seed (30 individuals per population) from plants growing in natural stands of *O. odorata* (ID 753, 35° 11′ 729″ S, 69° 47′ 396″ W, Las Leñas, Mendoza, 1828 m A.S.L), a hybrid (*O. odorata* × *O. mendocinensis* N, hereafter referred to as "hybrid"; ID 756, 35° 08′ 773″ S, 70° 04′ 690″ W, Las Leñas, Mendoza, 2256 m A.S.L.) and two populations of *Oenothera mendocinensis*, one native to the north-west of its range (hereafter referred to as *O. mendocinensis* N, ID 738, 33° 03′ 158″ S, 69° 17′ 201″ W, Tupungato, Mendoza, 2318 m A.S.L) and one native to the south-west of its range (hereafter referred to as *O. mendocinensis* S, ID 863, 46° 26′ 910″ S, 70° 12′ 781″ W, El Pluma, Santa Cruz, 464 m A.S.L) was collected. Voucher specimens are deposited at the PBP herbarium (Museo Egidio Feruglio, Chubut, Argentina).

2.2. Study site and experimental conditions

A single-factor field experiment, with a completely randomized design was conducted from March 19, 2003 to March 25, 2004 in Gaiman, Chubut, Argentina (43° 21′ 31″ S; 65° 38′ 39″ W). In this area the mean annual precipitation is 179 mm, mean low temperature of the coldest month (June and July) is 1 °C and absolute minimum air temperature is −10.8 °C. Seeds were initially sown in germination-trays filled with

soil, peat moss and sand in equal proportions and maintained in a greenhouse, where they received 80% of outside light levels and a temperature range of 25°/15 °C (average maximum daytime and average minimum nighttime temperature). Seedlings were transplanted to the field 45 days after sowing. Experimental units consisted of plots (4 plots/taxon for a total of 16 plots) of 10 rows, each including 15 plants, for a total of 150 plants per plot, and 600 plants per taxon. Plant density was 26 plants $* \text{m}^{-2}$, with rows 0.30 m apart and 0.15 m between plants. Each taxon was randomly assigned to four plots. Plots were flood irrigated every 15 days. Weed control was done by hand pulling.

classification of the flower supporting structures as vegetative or reproductive. The case of rosette plants in which the flowering spike bears cauline leaves is particularly controversial (see Thompson and Stewart, 1981 for a review). According to these authors and to Reekie and Bazzaz (1987), the least ambiguous definition is to consider all structures not possessed by the vegetative plant, to be reproductive. Therefore, stems were considered as a reproductive support-structure. Roots and leaves were considered vegetative biomass. As an estimate of the resources actually committed to reproduction, reproductive effort (RE; Thompson and Stewart, 1981) was calculated as follows:

$$RE = (\text{Fruit biomass} + \text{reproductive support-structure biomass})/\text{total plant biomass}.$$

2.3. Sampling, variables and allometric relationships

After bolting, in order to determine fruit set, five flowers per plant (10 plants/plot; 4 plots/taxon) were labeled and visually checked every even day for ovary enlargement. Before harvesting whole plants, the youngest fully expanded leaves (5 reps/plant; 5 plants/plot; 4 plots/taxon) were clipped 2–3 h after sunrise, stored in plastic bags during transport to the lab and placed in water for rehydration (SLA > 10 $\text{m}^2 \text{kg}^{-2}$; Garnier et al., 2001). Leaf area was determined using UTHSCSA Image Tool for Windows, Version 2.02. After scanning, leaves were oven-dried until constant weight. Specific leaf area was calculated as the leaf area: leaf weight ratio. Leaf area ratio was calculated as: LAR = SLA $*$ LMR, where LMR is the fraction of the total plant biomass allocated to leaves (Lambers et al., 1997). A threshold LAR value of 3.6 $\text{cm}^2 * \text{g}^{-1}$ was used to place populations within the LAR group, as this value is often cited as the highest value found for herbaceous plants (Galmés et al., 2005; Veneklaas et al., 2002).

Whole plants were harvested (3 reps/plot; 4 plots/taxon), and leaves, stems and roots were separated and placed in an oven at 60 °C and weighed daily until constancy of weight. There is no consensus in the literature about the

We included stem biomass in our calculations of reproductive effort, because this is a more exact measure than others that consider only ''obvious'' reproductive structures, such as inflorescences or fruits (Reekie and Bazzaz, 1987).

The technique of allometric analysis (Coleman et al., 1994) was used to correct allocation patterns for possible size differences among plants. Allocation parameters were plotted against the total biomass of the plants (Poorter and Nagel, 2000). For assessing for size-dependant variation in RE, we tested the null hypothesis that the intercept with the Y-axis $a = 0$ or, in other words that total plant mass and reproductive effort were proportional (Klinkhamer et al., 1990).

2.4. Chemical analysis

Total non-structural carbohydrates were determined by autoclaving (0.1 Mpa, 15 min) 50 mg of biomass in 100 ml of distilled water. Samples were homogenized in 100 ml of water and the dissolved sugars were determined by the anthrone method (Yemm and Willis, 1954).

Table 1 – Results of one-way ANOVA for morphological, vegetative and reproductive attributes of four taxa of Oenothera, grown under identical conditions, in the Chubut River Valley. Factor is population, with four levels. LAR = leaf area ratio; SLA = specific leaf area; TNC = total non-structural carbohydrates. Asterisk (*) indicates that variables were log transformed prior to analysis. Data is mean ± S.E. Different letters indicate significant differences between means (P < 0.05). Comparison of means among populations were assessed by Tuckey's test

Variable	df	F test	P value	High-LAR group		Low-LAR group	
				O. mendocinensis S	O. odorata	O. mendocinensis N	Hybrid
LAR (cm$^2 * $g^{-1})	3	81.17	<0.01	4.01 ± 0.13 c	4.05 ± 0.12 c	0.9 ± 0.12 a	1.63 ± 0.28 b
SLA (m$^2 * $kg^{-1})	3	3.53	0.06	15.09 ± 0.17 a	14.02 ± 0.52 a	17.71 ± 1.1 a	16.54 ± 1.08 a
Vegetative biomass (g)*	3	38.05	<0.01	4.57 ± 0.61 c	3.97 ± 0.46 c	0.92 ± 0.06 a	2.88 ± 0.37 b
Total biomass (g)*	3	3.10	<0.01	10.78 ± 1.31 ab	9.90 ± 0.97 a	8.87 ± 0.94 a	15.85 ± 2.5 b
Fruit Set	3	1.87	0.276	0.7 ± 0.01 a	0.8 ± 0.1 a	0.9 ± 0.01 a	0.95 ± 0.07 a
Reproductive Effort	3	87.29	<0.01	0.58 ± 0.03 a	0.59 ± 0.02 a	0.89 ± 0.01 c	0.81 ± 0.01 b
Root TNC (%)	3	35.28	<0.01	23.6 ± 0.7 c	21.9 ± 0.2 bc	13.7 ± 0.9 a	19.3 ± 0.9 b

2.5. Data analysis

The field experiment was analyzed using a one-way ANOVA with population (four levels) as the factor. Comparison of means among populations was assessed by Tukey's test. All analyses were done using Statgraphics Plus 5.0 (Statistical Graphics Corp.). In order to achieve normal distributions and homogeneous variances before performing parametric analysis, log transformation was applied to vegetative and total plant biomass (Gómez and Gómez, 1984). Biomass allometric relationships between each biomass fraction and total plant weight were assessed through linear regression models, following Coleman et al. (1994). As the x-intercepts did not significantly differ from zero, regressions were forced through the origin. Partitioning coefficients were assessed as the slope of the linear regressions. Slopes and means were compared using one-way ANOVA.

To test for proportionality in the reproductive effort of plants we used an F-test (Klinkhamer et al., 1990).

To test for direct and indirect effects of leaf attributes (SLA; LAR) on reproductive effort and carbohydrate storage, a path analysis was performed using the program package AMOS (Arbuckle and Wothke, 1999).

3.   Results

The evaluation of leaf allocation, assessed here as leaf area ratio (LAR), allowed us to divide *Oenothera* taxa into two groups: low-LAR (*O. mendocinensis* N and the hybrid) and high-LAR (*O. mendocinensis* S and *O. odorata*; Table 1). Differences in LAR were due to variation in the fraction of total plant weight allocated to leaves, because the specific leaf area (the morphological component of LAR) did not differ among groups (Table 1). As differences were found in total plant dry weight (Table 1), an allometric analysis of biomass partition was performed. No departures from linearity were found for any allometric relationship (Fig. 1), revealing that allocation increased linearly with plant size. Two different patterns of allocation were found: the high-LAR group allocated resources preferentially to growth and storage while the low-LAR group devoted more resources to reproduction (Tables 1 and 2). Vegetative biomass was significantly higher in the high-LAR group, while no significant differences were observed for root and leaf biomass partition coefficients within the group (Table 2). Together with this high allocation to vegetative structures, a low reproductive effort was observed (Table 1). An alternative life-history tactic, found in the second group of species, revealed a high reproductive effort (Table 1) combined with a low allocation to carbohydrate reserves. In our experiment, no differences in fruit set were found among taxa (Table 2), indicating that the high partitioning coefficients to fruit and stem biomass (assessed as the slope of the relationship, Fig. 1) were responsible for differences in reproductive effort. When testing for size dependant variation in reproductive effort, both groups showed a constant ratio RE/vegetative biomass, indicating a proportional allocation with size (Fig. 2a,b).

To gain more insight into the relative contribution to life history of morphological attributes and allocation pattern,
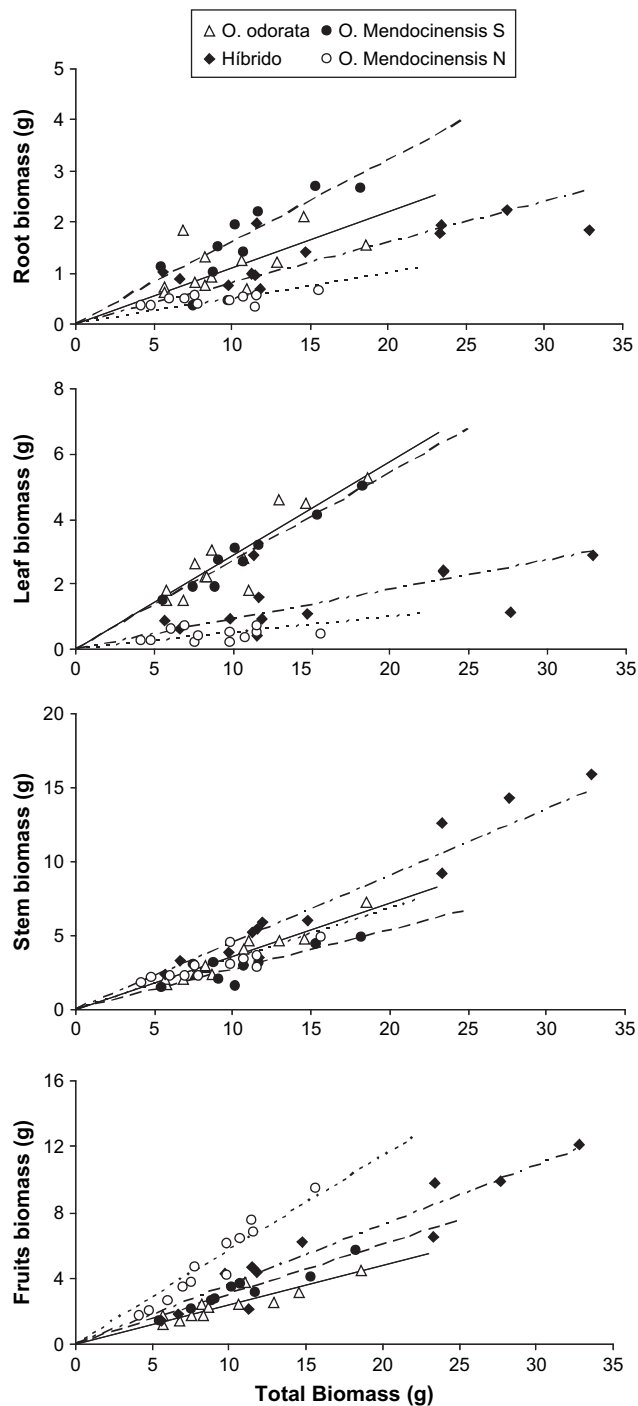

Fig. 1 – Allometric relationships between organ biomass fractions and total plant biomass for four taxa of *Oenothera* cultivated in a common garden. Regression coefficients (β) from linear fitting slopes are included in Table 2.

a path analysis was performed for both groups (Fig. 3). The standardized regression coefficients allow an estimation of how a change of one unit standard deviation of one variable affects another variable (also expressed in units of standard deviation), independent of other variables. For the high-LAR group (Fig. 3a), leaf area ratio appeared to be the most important factor explaining variation in storage and reproductive

Table 2 – Results of one-way ANOVA for regression coefficients (β) from linear fitting slopes of allometric relationships between organ biomass fractions and total plant biomass of four taxa of *Oenothera*, grown under identical conditions, in the Chubut River Valley. Beta coefficients are presented ±S.E. Different letters indicate significant differences between slopes for each biomass fraction ($P < 0.05$)

Variable	df	F test	P value	High-LAR group		Low-LAR group	
				O. mendocinensis S	*O. odorata*	*O. mendocinensis* N	*Hybrid*
Root biomass (g)	3	3.32	0.04	0.16 ± 0.01 b	0.11 ± 0.01 ab	0.05 ± 0.004 a	0.08 ± 0.01 a
Leaf biomass (g)	3	5.43	0.03	0.27 ± 0.01 b	0.29 ± 0.02 b	0.05 ± 0.01 a	0.09 ± 0.01 a
Stem biomass (g)	3	8.68	0.01	0.27 ± 0.01 a	0.36 ± 0.02 b	0.34 ± 0.01 ab	0.45 ± 0.02 b
Fruit biomass (g) (capsules + seeds)	3	3.23	0.04	0.13 ± 0.01 a	0.11 ± 0.01 a	0.24 ± 0.01 b	0.16 ± 0.01 b

effort (Table 3), with increasing leaf area ratio having a negative influence on storage (direct coefficient = − 0.41; Fig. 3a). However, due to an indirect effect through reproductive effort, an increase in leaf area ratio decreases reproductive effort, and this, in turn increases TNC, thus masking the negative direct effect of leaf area ratio on TNC (Table 3). Adding both the direct and indirect effects together, a negative total effect of leaf area ratio on reproductive effort was found. Specific leaf area had a significant and positive effect on reproductive effort, and no effect on TNC. Interestingly, vegetative biomass accumulation had no significant total effect either on reproduction or on storage (Table 3). Reproductive effort had a significant negative effect on TNC (Fig. 3a).

Leaf area ratio showed the same negative effect on reproductive effort in the low-LAR group, though no significant effect was found on TNC (Fig. 3b). Vegetative biomass was the only variable significantly correlated to TNC (Table 4). Specific leaf area showed a significant negative direct effect on vegetative biomass but no effect on reproductive effort (Fig. 3b).
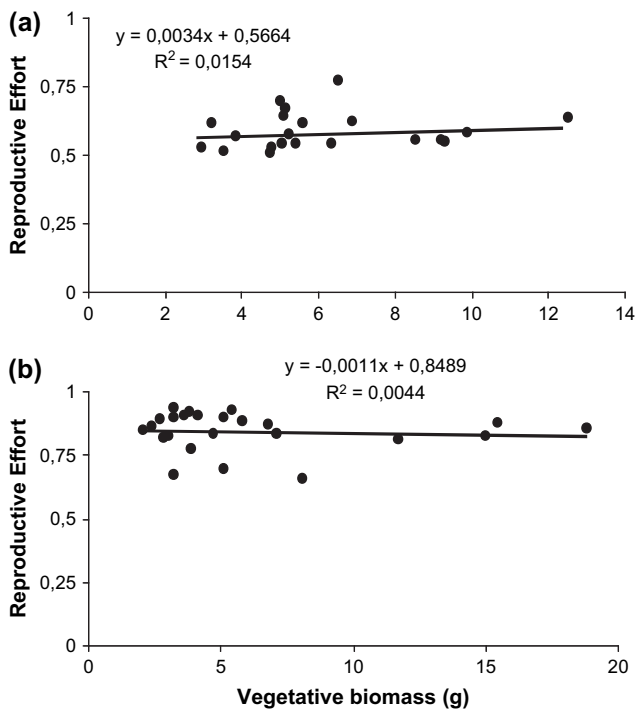
4. Discussion

Allometric rules dictate how metabolic production and biomass are partitioned between different plant parts at the level of the individual (Obeso, 2004). The manner in which plants partition products of photosynthesis into various plant parts is important in determining growth rate, vegetative biomass
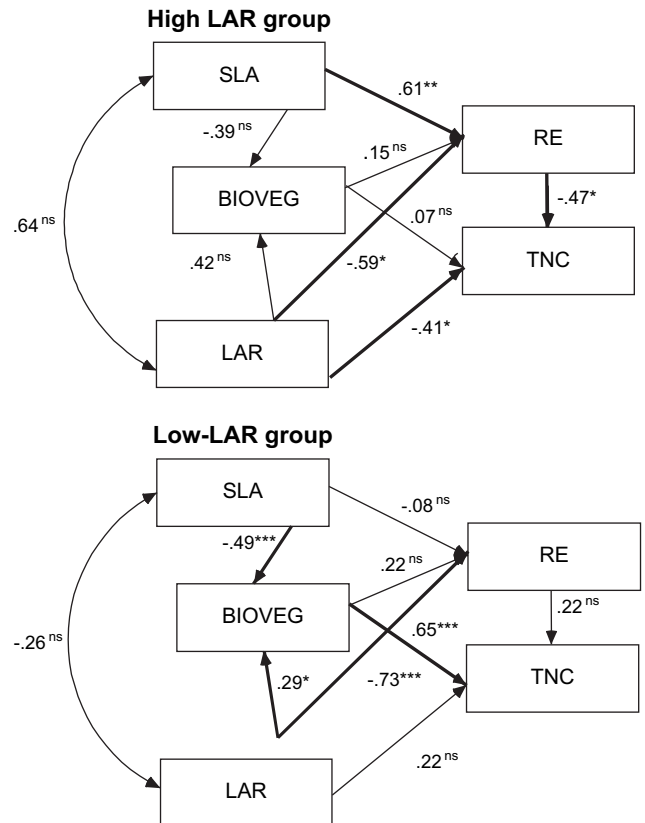
Fig. 3 – Path diagram showing the effects of leaves traits on reproduction and storage mediated by vegetative biomass. Asterisks indicate significance of the coefficient: three asterisks, P < 0.01; one asterisk, P < 0.05. Variation due to error is not included for simplicity. a) Model for *O. mendocinensis* S and *O. odorata* (high-LAR group); and b) Model for *O. mendocinensis* S and the hybrid (low-LAR group).

Fig. 2 – Size-dependent reproductive effort. a) High-LAR; and b) Low-LAR.

Table 3 – Total, direct and indirect path coefficients of the effects of leaf area ratio (LAR), specific leaf area (SLA) and log vegetative biomass (VEG BIO) on reproductive effort (RE) and total non-structural carbohydrates (TNC) of the high-LAR group (see Fig. 2a), calculated by using a path analysis. Bold numbers indicate significant coefficients ($P < 0.05$)

	Total effects		Direct effects		Indirect effects	
	RE	TNC	RE	TNC	RE	TNC
SLA	**0.671**	−0.346	**0.612**	0.000	0.059	−0.346
LAR	**−0.656**	**0.067**	**−0.593**	**−0.408**	−0.064	0.341
VEG BIO	−0.152	0.144	−0.152	0.072	0.000	0.072

and reproductive output (Brown, 1988). Since our field observations and literature (Kachi and Hirose, 1983) lead us to the supposition that leaf allocation was related to life history tactics in *Oenothera* taxa, we used leaf area ratio as the criterion for placing our taxa in two different groups: high- and low-LAR. The LAR is a composite parameter, partly determined by allocation (the fraction of total plant weight allocated to leaves) and partly by leaf morphology (SLA; Poorter and Remkes, 1990). Usually, both components of LAR are correlated positively with relative growth rate and biomass accumulation (Poorter, 1989; Poorter and Remkes, 1990; Poorter and de Jong, 1999). In our experiment, biomass allocation to the leaves was the factor responsible for differences in LAR because *Oenothera* taxa did not statistically differ in SLA. Despite similarities, positive and negative effects of SLA on reproductive effort were observed. This is difficult to account for, because the specific mechanisms behind that response remain to be elucidated.

We used LAR for path analysis, because the correlation with reproductive effort and TNC was not as good for leaf biomass as for LAR, in accordance to the findings of Poorter (1989). Path analysis confirmed our assumption and revealed that LAR is the most important variable in explaining variation in resource allocation to reproduction or storage among these taxa of *Oenothera*. As a larger LAR serves to capture more light (Lambers et al., 1997), more photosynthates are available to be allocated among three competing ends: vegetative growth, reproduction and storage as reserves (Chiariello and Roughgarden, 1984). In agreement with our hypothesis, the high-LAR group allocated photosynthates preferentially to vegetative growth and storage. As a result, plants in this group showed a higher vegetative biomass and more carbohydrate reserves than those individuals in the low-LAR group. This high allocation to growth was in conformity with the positive correlation expected between LAR and biomass accumulation (Poorter, 1989; Poorter and Remkes, 1990; Reich et al., 1992; Veneklaas et al., 2002), but this increase in size was not correlated, as expected, with an increase in reproductive

effort (Samson and Werk, 1986; Klinkhamer et al., 1990, 1992). As an alternative to the predicted pattern, carbon storage, a function generally associated with perenniality (Dina and Klikoff, 1974) was the preferred sink of photoassimilates for the high-LAR group and, as we predicted, a trade-off arose between reproductive effort and accumulation of reserves.

Alternatively, the low-LAR group allocated photosynthates preferentially to reproductive structures, showing the life history tactic of annual plants, for which storage of TNC does not seem to be a feasible option during the reproductive season, when reproductive effort is expected to be maximum (Hautekeete et al., 2001; Stearns, 1989). In this sense, the reproductive effort of this group was higher than that of the high-LAR group. Bearing in mind that much of the variation in RE may be due to size-dependent effects (Samson and Werk, 1986; Karlsson et al., 1990) and that we found significant differences in size between groups, and even between taxa within a group, we performed a test of proportionality and we found that RE does not change with plant size. A possible explanation to this pattern is that plants such as *Oenothera*, with a basal rosette-growth form, have to form a conspicuous flowering stalk before flowers and seeds can be produced, then; the production of the first seed brings about large overhead costs while the production of further seeds requires only a relatively small investment. This kind of situation gives the linear model we found (Fig. 2) in which total plant mass and reproductive mass are proportional (Klinkhamer et al., 1990).

For the low-LAR group, we found a positive relationship between vegetative biomass and TNC accumulation, where a trade-off was presumed because a reserve formation involves the synthesis of storage compounds from resources that might otherwise directly promote growth (Chapin et al., 1990). According to Van Noordwijk and de Jong (1986), significant positive correlations are sometimes found when negative correlations would be expected when variation among individuals in the allocation of resources is small or absent. Within the low-LAR group, little variation was found in allocation to vegetative biomass or carbohydrates reserves. At the same

Table 4 – Total, direct and indirect path coefficients of the effects of leaf area ratio (LAR), specific leaf area (SLA) and log vegetative biomass (VEG BIO) on reproductive effort (RE) and total non-structural carbohydrates (TNC) of the low LAR group (see Fig. 2b), calculated by using a path analysis. Bold numbers indicate significant coefficients ($P < 0.05$)

	Total effects		Direct effects		Indirect effects	
	RE	TNC	RE	TNC	RE	TNC
SLA	**−0.193**	−0.361	−0.084	0.000	−0.108	−0.361
LAR	**−0.666**	0.256	**−0.730**	0.217	0.064	0.039
VEG BIO	0.221	**0.697**	0.221	**0.648**	0.000	0.050

time, the increase of stores in late season may, possibly, not compete with growth, because for wild plants, it remains uncertain the extent to which seasonal fluctuations in stores reflect accumulation due to unfavorable conditions for growth, or reserves formed in competition with growth (Chapin et al., 1990).

Evans et al. (2005) found that evolution from the perennial to the annual habit in *Oenothera* occurs in response to increasingly arid environmental conditions. This work illustrates that the physiological capabilities of a particular population may cause life history to evolve in response to some aspects of aridity, for example, temperature. In this sense, it has been observed that annuals are not prevalent in cold deserts (Comstock and Ehleringer, 1992) like Patagonia. Accordingly, *O. mendocinensis* S, the southernmost studied population, showed the strategy of the perennial habit. Despite life-history theory suggesting which reproductive strategy is favored depends on the relative force of mortality on seedlings versus adults (Stearns, 1992), we reported here the coexistence of semelparous and iterouparous populations (*O. odorata* and *O. mendocinensis* N), as has previously been documented at dry sites in Hawaii (Robichaux et al., 1990).

5. Conclusions

On the basis of the results obtained in this study, we conclude that differences in leaf area ratio are related to disparities in the allocation pattern to two competing functions: storage and reproduction. *Oenothera* populations within the high-LAR group allocated resources preferentially to carbohydrate reserves, a tactic associated with perenniality, and a trade-off arose between reproductive effort and storage. Alternatively, populations within the low-LAR group allocated resources preferentially to reproductive structures, a strategy associated with annual plants. No evidence of trade-off between reproduction and storage was found in this group.

Acknowledgements

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