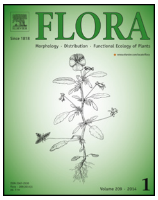
Flora 212 (2015) 1–9

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora



Carbon acquisition strategies uncoupled from predictions derived from species life-cycle

L. González-Paleo*, D.A. Ravetta

CONICET, Museo Egidio Feruglio, Av. Fontana 140, 9100 Trelew, Chubut, Argentina

ARTICLE INFO

Article history:
Received 13 June 2014
Received in revised form 4 February 2015
Accepted 14 February 2015
Edited by Hermann Heilmeier.
Available online 17 February 2015

Keywords:
Relative growth rate
C acquisition–conservation trade-off
Physaria
New crops
Arid environments
Functional traits

ABSTRACT

We compare carbon use strategies of congeneric annual (*P. gracilis* and *P. angustifolia*) and perennial (*P. mendocina* and *P. pinetorum*) *Physaria* (Brassicaceae), to evaluate the relevance of eco-physiological traits as determinants of differences in growth and to add information on the current debate on the agro-ecological suitability of perennial species for grain production in low resource ecosystems. Because of differences in growth and in seed-output previously found within this genus, we hypothesized that C acquisition strategies would not be fully coupled with predictions derived from a species life-cycle. Further, we expected to find different suites of traits related to C-acquisition among perennial species of *Physaria*. We found species with high (*P. gracilis* and *P. pinetorum*) and low (*P. mendocina* and *P. angustifolia*) relative growth rate (RGR) and biomass. The variation in RGR was linked to differences in specific leaf area (SLA) and allocation to leaves (leaf mass ratio, LMR) and roots (root mass ratio, RMR), but not to the species life-cycle. *Physaria gracilis* had high allocation to leaf area (leaf area ratio, LAR), LMR, high SLA, and low RMR and carbohydrates reserves. The slow-growth strategy found in *P. mendocina* was linked to low LAR, low SLA and large below-ground allocation. The other species showed intermediate strategies between these two. The sets of traits present in *P. gracilis* and in *P. mendocina* are extremes in the C acquisition–conservation trade-off, and may allow them to cope with low resource environments in different ways. SLA, LMR and RMR were the main determinants of RGR, while total non-structural carbohydrates (TNC) and leaf longevity were linked to the life-cycle. Taken together these characters define the intermediate growth strategies of *P. angustifolia* and *P. pinetorum*. These intermediate strategies were not dependent on the species life cycle and support the hypothesis of uncoupled relationships between growth, C acquisition strategies and life-cycle.

Introduction

Biomass, growth rate and the suite of traits associated, are central to models in plant ecology because they are key determinants of plant performance, including reproduction, survival, and competitive ability (Tilman, 1988; Westoby, 1998; Grime, 2001; Pino et al., 2002). They also determine the adjustment of plants to environments differing in resource availability (Lambers et al., 1998). Thus, studies that undertake comparative ecology of plants which differ in growth rate are critical to evaluate and improve such ecological models. Furthermore, these studies have many uses in agricultural practice and implementation, and due to the extent to which the suites of traits related to growth vary among species, set limits on biomass production and utilization (Poorter et al., 2012). Much empirical work has focused on the search of morphological (leaf area ratio – LAR; specific leaf area – SLA; the allocation pattern to root, root mass ratio – RMR; total non-structural carbohydrates – TNC; and leaf, leaf mass ratio – LMR), and physiological (photosynthetic rate – A, or net assimilation rate – NAR) correlates of relative growth rate (RGR; Grime and Hunt, 1975; Poorter, 1989; Reich et al., 1998; Shipley and Meziane, 2002). Still, the relevance of the variation in relative importance of underlying components to RGR and biomass is not well understood. Variation in leaf and root structure appears to influence growth more strongly than biomass partitioning and physiological activity (Reich et al., 1998). However, the pattern is complex, and the critical correlate may depend on resource levels (Meziane and Shipley, 1999; Shipley, 2002), or on which life-forms (i.e., trees, shrubs, grasses, and perennial and annual forbs) are being compared (Marañon and Grubb, 1993). The majority of comparative experiments published in relation to life-cycle are restricted to grasses (Garnier, 1992; Garnier and Laurent, 1994), and in most cases, comparisons between annual and perennial forbs failed to identify differences in biomass allocation, SLA, and growth (Poorter et al., 2012).

---

* Corresponding author. Tel.: +54 2804432100; fax: +54 2804 462100.
E-mail address: lgonzalezpaleo@mef.org.ar (L. González-Paleo).

http://dx.doi.org/10.1016/j.flora.2015.02.004
0367-2530/

The structure and morphology of plant organs, and the resource allocation pattern appear to be to some extent determined by a trade-off between growth and survival (Metcalf et al., 2006; Poorter and Bongers, 2006; Patty et al., 2010). This trade-off reflects different ecological plant strategies that determine that individuals achieve some capabilities at the expense of others (Grime, 1979; Weiner, 2004; Hautekeete et al., 2009). The optimal values of other morphological, physiological, and phenological traits differ according to life-form and provide different mechanisms to adapt to their environments (Lambers and Poorter, 1992). Within this context, it is expected that annual and perennial forbs will differ in their plant growth strategy and in their ability to capture, use, and conserve resources such as carbon.

Annual species have to reproduce within a single growing season, a pattern that requires relatively fast growth, and is allowed by a large biomass investment in thin, highly productive leaves, with high nitrogen concentrations and a high photosynthetic capacity (Arendt, 1997). This fast-growth strategy allows annuals to capture and utilize resources better than perennials, when resources are not limiting. On the other hand, perennial forbs are perceived as having a slow-growth strategy as a result of the trade-off between growth and survival. They would possess morpho-physiological traits, such as the formation of thick, well-protected leaves, and a large root system for below-ground carbohydrate and nutrient storage, which enhance survival and protection of limiting resources (Canham et al., 1999), at the expense of a reduced capacity for growth (Chapin et al., 1993).

We present a comparative analysis of biomass allocation, morphology and leaf physiology for congeneric annual and perennial *Physaria* (Syn *Lesquerella*; Brassicaceae), to study the relevance of functional and structural traits as determinants of differences in growth and carbon use strategies among species that differ in life-cycle. Specifically, we aim to answer the following questions: (1) is the variation in morpho-physiological traits related to growth associated with the plant's life-cycle? (2) do the relationships between growth, carbon use strategy and life-cycle respond to the trade-off between growth and survival?

We focused on the genus *Physaria* because it includes annual, biannual and perennial species native of arid lands (Rollins and Shaw, 1973), and thus, provides a suitable system for comparative studies among species that differ in their life-cycle (Hautekeete et al., 2001). This genus has also been used as a model for the understanding of the domestication of new oil-seed crops for arid lands (Dierig et al., 1993; Ravetta and Soriano, 1998). This comparison is not only relevant for the understanding of intrinsic differences in plant growth between annual and perennial desert forbs, but could also help sort out a current debate on the agro-ecological usefulness of perennial species in low resource ecosystems (Pimentel et al., 2012). Both annuals and perennials have been evaluated for their productive potential mostly in low-resource environments, but with high-input supplements (water and fertilizers). Under these conditions annual *Physaria* species are preferred because of their higher productivity (biomass, seed and oil yield; Dierig et al., 1993). The slow-growth strategy and high resource use-efficiency of perennials (Chapin, 1980; Arendt, 1997) should allow dealing with the low resource availability characteristic of arid environments, without the need for massive resource supplementation, and conserving ecosystem processes such as water and nutrient cycling, C sequestration, and soil erosion (DeHaan et al., 2005). The main constraint to incorporate perennials as grain crops is that their biomass production and seed yield are actually lower in several perennial weeds compared with a closely related annual crop (Benech Arnold et al., 1992; Vilela et al., 2008). Still, in some cases perennials have presented attributes that show high productivity while maintaining perenniality (Ploschuck et al., 2001; DeHaan et al., 2005; DeHaan and Van Tassel, 2014). The understanding of the functional basis (morphological and physiological) is thus, relevant to identify key traits that guide the improvement of productivity in perennials. Because of differences in growth and seed-output previously found within this genus (González-Paleo and Ravetta, 2011; Masnatta and Ravetta, 2011), we hypothesized that carbon acquisition strategies would not be fully coupled with predictions derived from a species life-cycle. Even when they maintain their perennial cycle, we expect that not all perennial *Physaria* species have the same suite of traits related to C acquisition which are key determinants of plant productivity.

Materials and methods

Plant material and experimental design

We performed a factorial field experiment in a common garden in the Chubut River Valley, Patagonia Argentina (43°21′31″S; 65°38′39″W). To test consistency of differences among species in the trait set evaluated, we replicated the experiments during two years: 2006/2007 (year 1) and 2007/2008 (year 2). A set of morphological and physiological traits related to the C economy and their relationship with growth were determined for a group of annual and perennial *Physaria* (Brassicaceae) species. *Physaria* plants have an acaulescent rosette in the vegetative state, which develops elongate stems bearing leaves, flowers and capsules in the reproductive state. We evaluated two annual species native to Oklahoma and Texas: *P. gracilis* (Hook.) Wats. and *P. angustifolia* (Nutt.); and two perennial species: *P. pinetorum* Wooton & Standley native to Arizona, and *P. mendocina* (Phil) Kurtz, native to Argentina (La Pampa), all grown in a common garden experiment (see Section *Study site*). The areas to where these species are native and from where seeds were collected have similar environments regarding water availability: low total annual precipitation (200–400 mm), winter–spring seasonality, and a clear summer water deficit (González-Paleo, 2010).

For both experiments, seeds of wild accessions of each species (bulk of 10 wild populations of each species) were harvested and stored at 4 °C, until they were sown in germination-trays filled with soil: peat moss: sand, in equal proportions and maintained in a greenhouse, where they received 80% of outside photosynthetic active radiation levels (2100 μmol m^{-2} s^{-1}). Temperature in the greenhouse ranged between 25 and 15 °C (average maximum daytime and average minimum nighttime temperature, respectively). Seedlings were transplanted to the field 66 (April 21, 2006) and 72 (May 2, 2007) days after sowing, for year 1 and 2, respectively.

In this common garden experiment, experimental units were plots (70 m × 0.75 m) in a completely randomized experimental design with one factor (plant species; 6 plots per species, 4 species of *Physaria*). Plants within plots were arranged in rows 0.4 m apart and 0.17 m between plants. Each of the 6 experimental units (plots) included 8 plants per species (for a total of 48 plants per species). Density was low enough (16 plants m^{-2}) to avoid detrimental effects of competition on final biomass, probability of flowering and reproductive allocation (Brahim et al., 1998). Weeds were removed manually, to avoid competition.

Study site

The experimental site is located at Trelew (Argentina), in the ecotone between the Monte and the Patagonia phytogeographical regions. The climate type is Mediterranean, with a notable wet season in fall and winter, while summers are hot and dry. In this area the mean annual precipitation is 178 mm, the mean annual temperature is 13.3 °C, the mean minimum temperature is 6.9 °C and the mean maximum temperature is 20.1 °C (Cabrera, 1994), the average daily photosynthetic photon flux density at midday is 2100 μmol m^{-2} s^{-1}. The soil water-balance is negative through the year but more significantly from late spring to the end of summer, when the plants received a subsidiary irrigation. Plots were irrigated once a month from September, 21 until the end of the growth cycle (late February). Enough water was applied on each irrigation to saturate the upper 50 cm of the soil profile. This amount of water and frequency of irrigation was enough to prevent plants to reach a severe water deficit and die from drought stress.

There were significant differences in meteorological conditions between the two years, mainly during the vegetative period (autumn–winter). Due to the negative annual water balance plant growth relies on water accumulated in the soil profile during winter months. Because of the differences in the amount of water accumulated during winter and differences in atmospheric demand in spring and summer, the environmental conditions can widely vary between years and so does the response of the plants. Experiment 1 was performed under an average year: both annual mean precipitation (184 mm) and minimum mean temperature (6.2 °C) were within the range of 1.5 standard deviation (S.D.) of the mean historical values for the study site. However, Experiment 2 was performed during a drier and cooler year, 153 mm and 3.6 °C, for annual mean precipitation and minimum mean temperature, deviating 3 and 8 S.D. of the mean for the area, respectively.

Growth analysis

Allocation pattern

We performed five harvests of six plants per species (1 plant per plot) corresponding to five phenological stages: (1) vegetative rosette (166 days after seeding – DAS), (2) floral bud (202 DAS), (3) anthesis (240 DAS), (4) fructification (283 DAS), and (5) maturity (334 DAS). The methodology of comparing traits based on phenological stage is considered appropriate to eliminate the effect of ontogeny on interspecific differences in relative growth rate and growth related traits (Coleman et al., 1994).

Each individual's biomass was fractionated into roots, leaves and reproductive structures (floral stems, fruits and seeds). Total leaf area per plant was determined using UTHSCSA Image Tool for Windows, version 2.02. After scanning, plant samples were dried at 70 °C for 48 h and weighed. We estimated the proportional allocation to leaves (LMR; g leaf/g total biomass), to roots (RMR; g root/g total biomass) and to reproductive biomass (harvest index; g reproductive structures/g total biomass). These data were used to calculate specific leaf area (SLA, cm^2 of total leaf area/g leaf), leaf area ratio (LAR, cm^2 total leaf area/g total biomass), net assimilation rate (NAR, mg m^{-2} d^{-1}, Eq. (1), and relative growth rate (RGR, mg g^{-1} d^{-1}, Eq. (2); Hunt et al., 2002) for three periods: (1) pre-anthesis (from vegetative rosette until anthesis), (2) post-anthesis (from anthesis until maturity), and (3) overall RGR (entire cycle, from vegetative rosette to maturity).

$$\mathrm{NAR}(\mathrm{mg\,m^{-2}\,d^{-1}}) = \frac{(B_2 - B_1) \times (\ln \mathrm{LA}_2 - \ln \mathrm{LA}_1)}{(t_2 - t_1) \times (\mathrm{LA}_2 - \mathrm{LA}_1)} \tag{1}$$

$$\mathrm{RGR}(\mathrm{mg\,g^{-1}\,d^{-1}}) = \frac{\ln B_2 - \ln B_1}{t_2 - t_1} \tag{2}$$

where B is total biomass, and LA is total leaf area, at time 1 and 2, respectively (t_1 and t_2).

Phenology

The number of days from emergence to rosette, anthesis and maturity was recorded for all plants. The criteria used to decide the moment in which a species had reached anthesis and maturity was when 50% of the plants of a plot had at least one flower or one mature fruit, respectively.

Leaf longevity was measured on one leaf per plant. Recently emerged leaves were marked and monitored weekly, and classified as green or senescent. A leaf was considered dead when more than 50% of leaf lamina was chlorotic (dark yellow). Leaf longevity was expressed in weeks, from leaf appearance to leaf senescence.

Chemical analysis

For carbohydrate determinations, root dry samples (125 mg each) were extracted with 70 ml of 10% (v/v) chlorhydric acid at 100 °C for an hour. The extract solution was collected and brought to a final volume of 100 ml. Soluble sugars were determined using anthrone, according to the method of Yemm and Willis (1954). Six root samples were extracted for each species (1 plant per plot). Carbohydrate storage was measured in roots only because this organ can store more TNC reserves and it is a more sensitive measure of accumulated C reserves than stems (Vilela and González-Paleo, 2015). The vegetative stems are very small in species forming a rosette during the first growth cycle, and do not accumulate a significant proportion of reserves.

Gas exchange

In year 1, instantaneous CO$_2$ assimilation rate (A) and transpiration rate (E) were measured every two hours, from sunrise to sunset, on individual leaves of six plants at anthesis (1 plant per plot), using an infrared gas analyzer (LCA-4, ADC, Hoddeson, England). Measurements were made on leaves fully exposed to direct sunlight, and maintained perpendicular to the incident solar radiation. Mean air temperature and humidity were 26.5 °C and 81%, respectively. CO$_2$ concentration was 395 μl l^{-1}. The values of daily net CO$_2$ assimilation and E were obtained integrating the values of instantaneous CO$_2$ assimilation rate (A) and transpiration, respectively. Leaf water use efficiency (WUE) was estimated for each sample by calculating the A/E ratio for integrated values.

Statistical analysis

To test for differences in RGR and NAR between species we performed a two-factor analysis of variance (species and time), with ln transformed plant total weight or total leaf area, as the dependent variables, respectively. Significant species × time interaction indicates differences in RGR or NAR (slopes; Poorter and Lewis, 1986).

Analysis of variance with two factors (species and year) was used to determine differences in the morpho-physiological traits between species and among years of experiment (interaction species × year). When significant species × year interactions were detected, one-way ANOVA and Tukey's test were performed for each year, in order to explore differences between annuals and perennials species. To check for data normality we used Shapiro–Wilk's test and Levene's test for homogeneity of variance. A natural logarithm (for LMR and total biomass) or square-root (for RMR) transformation was applied when necessary to satisfy the assumptions of ANOVA.

To investigate the relationships between the suites of traits and RGR and total biomass, we performed a path analysis for annuals and perennials together using the program package AMOS (Arbuckle and Wothke, 1999). Path analysis is a form of multiple regression that allows consideration of complex causal structures with more than one dependent variable on another (Mitchell, 1992), and thus, allows for testing of a priori defined direct and indirect causal relationships.

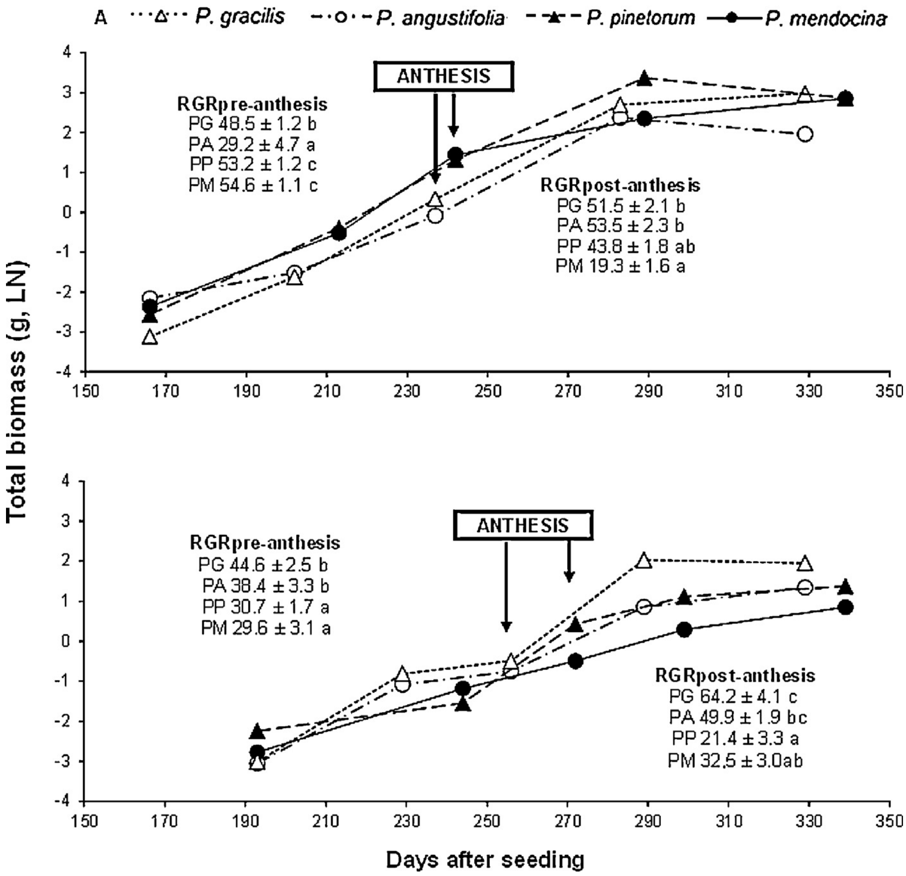


Fig. 1. Total biomass per plant in annual (*P. gracilis*, PG; and *P. angustifolia*, PA) and perennial (*P. pinetorum*, PP; and *P. mendocina*, PM) species of *Physaria* for (A) 2006–2007 and (B) 2007–2008 growth season, in five phenological stages (rosette, bud appearance, anthesis, fructification and physiological maturity). Relative growth rate (RGR) for the pre- and post-anthesis period is also shown.

Results

Growth capacity: relative growth rate and biomass

Differences in environmental conditions between the two years resulted in differential growth responses within the group of species of *Physaria* (significant interaction species × year). In year 1, *P. gracilis* and *P. pinetorum* had higher RGR total than *P. angustifolia* and *P. mendocina* (Table 1). The seasonal growth pattern also differed: perennials had higher RGR pre-anthesis while annuals showed higher RGR post-anthesis (Fig. 1a).

In year 2 the ranking of species with high or low RGR was different to that of year 1. While RGR for both annuals was similar to that found in year 1, RGR of both perennials was significantly lower in year 2 (27% lower in Experiment 2 than in Experiment 1; $p < 0.01$; Table 1), which was characterized by drier and colder conditions. This decrease in RGR found in both perennials was determined mainly by a decrease in RGR pre-anthesis (Fig. 1a and b). Overall, in year 2, we found a gradient in RGR, from the annual, *P. gracilis* with the highest RGR, to the perennial, *P. mendocina* with the lowest RGR, and with *P. angustifolia* and *P. pinetorum* in between the two extremes (Table 1).

The pattern of interspecific variation in total biomass was similar to that of RGR (Table 1), with marked differences within annuals and perennials in year 1, and a gradient in year 2. Also, the decrease in total biomass from year 1 to 2 was lower (50% reduction) in annuals than in perennials (80% reduction).

Morpho-physiological traits

Leaf traits

We found significant differences between species in the set of leaf structural and functional traits associated with growth rate. In year 1, *P. gracilis* had higher LAR and SLA than the other species

Table 1
Relative growth rate (RGR) and total biomass for total growth cycle, for annual (*P. gracilis* and *P. angustifolia*) and perennial (*P. pinetorum* and *P. mendocina*) species of *Physaria*. Differences among species were evaluated for each year because the interaction between species and year was significant for both RGR and total biomass ($p < 0.05$, not shown). Data indicate means ± S.E ($n = 6$).

		P. gracilis	*P. angustifolia*	*P. pinetorum*	*P. mendocina*	*F* test
Year 1	RGR[a] ($mg\,g^{-1}\,d^{-1}$)	52.5 ± 8.6b	39.1 ± 5.3a	49.1 ± 4.5b	37.3 ± 9.3a	$6.3^{**,a}$
	Total biomass (g)	13.2 ± 0.6b	8.2 ± 0.9a	21.9 ± 2.1b	11.3 ± 1.3a	7.5^{***}
Year 2	RGR[a] ($mg\,g^{-1}\,d^{-1}$)	49.5 ± 14.6c	36.3 ± 13.4b	32.9 ± 7.0b	29.9 ± 8.2a	$3.4^{*,a}$
	Total biomass (g)	7.4 ± 1.1c	3.7 ± 0.8b	3.6 ± 0.5b	1.9 ± 0.4a	13.6^{***}

ns, non-significant.

[a] Significant difference in RGR between species was evaluated using *F* test corresponding to species × time interaction.

[*] $p < 0.05$.

[***] $p < 0.001$.

(Table 2A). Perennials did not differ in LMR from *P. gracilis*, but the high SLA of the annual determined its higher LAR compared to the perennials. The other annual, *P. angustifolia*, had the lowest values for LAR and LMR (Table 2A). Annuals had lower leaf longevity than perennials (Table 2A).

In year 2, both annual species and *P. mendocina* had lower LMR than *P. pinetorum*. The latter together with *P. gracilis* showed higher LAR than *P. mendocina* and *P. angustifolia*. The annual *P. gracilis* compensated the lower leaf biomass allocation with higher SLA. The ranking in SLA among the four species followed the same pattern as RGR and total biomass: lowest for *P. mendocina*, highest for *P. gracilis* and intermediate in *P. angustifolia* and *P. pinetorum* (Table 2B).

In year 1, net assimilation rate was higher in perennials than in annuals. This pattern was reverted in the second experiment, in which both annual species had higher NAR than perennials (Table 2A and B).

Root traits

The environmental differences between the two years of experiment resulted in changes in the patterns of below-ground allocation between species.

For year 1, both annual species had lower RMR and TNCveg than both perennials (Table 2A). This pattern was different for year 2: *Physaria mendocina* had the highest RMR of the four species, while *P. gracilis* allocated the lowest proportion of all four species to roots (Table 2B). *Physaria angustifolia* and *P. pinetorum* had RMR values intermediate to *P. gracilis* and *P. mendocina*, following the pattern that was found for RGR. We did not find differences among species in TNCveg.

While we did not find differences in pre-anthesis storage between species in year 2, post-anthesis storage was larger in perennials than in annuals in both years (Table 2B). Seasonality in carbohydrate reserves was not found for annuals; on the other side, post-anthesis storage was 60% higher in relation with pre-anthesis storage for perennials in the second year.

Generative traits

Differences among species in reproductive biomass and harvest index were analyzed for each year separately because we found significant species × year interactions ($p = 0.025$ and $p = 0.011$, respectively). For year 1, allocation to reproductive structures and harvest index were higher for annuals and the perennial *P. pinetorum* than for *P. mendocina* (Table 3A). In year 2, reproductive biomass and harvest index followed the same pattern as for RGR and biomass: highest in the annual *P. gracilis*, lower in the perennial *P. mendocina*, and with *P. angustifolia* and *P. pinetorum* in between the two extremes (Table 3B).

Determinants of RGR and total biomass

A path analysis was performed to identify the structural and functional basis of variation in RGR and total biomass between species. The path analysis revealed X^2 values of 10.09 ($p = 0.34$) and 13.53 ($p = 0.14$) for years 1 and 2, respectively, indicating that the proposed models adequately described the underlying relationships of the path model.

The variation in RGR was explained mainly by differences in specific leaf area (SLA), and root allocation (RMR). In year 1, LAR was determined by its two components: LMR and SLA, but the path coefficient was stronger for SLA than for the former (Fig. 2A). In year 2, LAR was only associated with the proportional allocation to leaf (LMR). SLA had a direct effect on RGR (Fig. 2B).

Specific leaf area (SLA) caused contrasting effects on total biomass depending on the path to be followed. On one side, SLA was positively linked to total biomass through an indirect effect on LAR and/or RGR (Fig. 2A and B). On the other side (although only in the year 1), we found an indirect negative relationship between SLA and total biomass through NAR (net assimilation rate). The latter indirect effect was less important (lower indirect coefficient

Table 2

Characterization of leaf and root traits for annual (*P. gracilis* and *P. angustifolia*) and perennial (*P. pinetorum* and *P. mendocina*) species of *Physaria* for: (A) year 1 and (B) year 2. LAR, leaf area ratio; SLA, specific leaf area; LMR, leaf mass ratio; NAR, net assimilation rate; Ad, daily CO_2 assimilation rate; RMR, root mass ratio; TNC_v, vegetative total non-structural carbohydrate; and TNC_R, reproductive total non-structural carbohydrate. Ad and leaf longevity were measured only during year 1. Differences among species were evaluated for each year because the interaction between species and year was significant for all traits ($p < 0.05$, not shown). Data are means ± S.E ($n = 6$).

(A) Year 1	*P. gracilis*	*P. angustifolia*	*P. pinetorum*	*P. mendocina*	*F* test
Leaf traits					
LAR ($cm^2\,g^{-1}$)	83.3 ± 2.9b	62.3 ± 2.3a	68.6 ± 3.2a	69.2 ± 5.9a	7.5[**]
SLA ($cm^2\,g^{-1}$)	142.1 ± 4.7b	113.8 ± 4.4a	109.0 ± 5.8a	97.0 ± 10.8a	4.2[**]
LMR ($g\,g^{-1}$)	0.63 ± 0.03ab	0.58 ± 0.02 a	0.66 ± 0.02b	0.63 ± 0.02ab	3.1[*]
Leaf longevity (weeks)	10.9 ± 0.3a	10.8 ± 0.3a	23.5 ± 0.9b	22.8 ± 0.8b	23.2[***]
NAR ($mg\,m^{-2}\,d^{-1}$)	5.1 ± 0.9a	5.3 ± 1.3a	9.4 ± 0.3b	10.0 ± 0.6b	2.84[*,a]
Ad ($mmol\,cm^{-2}\,d^{-1}$)	376.9 ± 43.1a	371.8 ± 51.7a	441.5 ± 47.1a	414.9 ± 47.4a	3.4[*]
Root traits					
RMR ($g\,g^{-1}$)	0.03 ± 0.003a	0.02 ± 0.002a	0.04 ± 0.002 ab	0.06 ± 0.005b	9.4[**]
TNCv (%)	8.3 ± 0.3a	7.8 ± 1.1a	15.6 ± 0.3b	22.8 ± 0.5c	12.9[***]
TNCr (%)	9.5 ± 1.0a	9.7 ± 1.1a	14.5 ± 2.6b	17.3 ± 1.1b	9.7[**]
(B) Year 2	*P. gracilis*	*P. angustifolia*	*P. pinetorum*	*P. mendocina*	*F* test
Leaf traits					
LAR ($cm^2\,g^{-1}$)	83.8 ± 8.3b	59.5 ± 2.4a	82.1 ± 5.0b	76.0 ± 3.2ab	6.4[**]
SLA ($cm^2\,g^{-1}$)	170.5 ± 24.8c	119.8 ± 5.2b	119.5 ± 8.0b	90.7 ± 6.7a	5.8[**]
LMR ($g\,g^{-1}$)	0.57 ± 0.04a	0.49 ± 0.03a	0.71 ± 0.03b	0.57 ± 0.03a	5.9[**]
NAR ($mg\,m^{-2}\,d^{-1}$)	5.8 ± 0.52c	6.5 ± 0.93c	4.7 ± 0.30b	3.2 ± 0.40a	3.1[*,a]
Root traits					
RMR ($g\,g^{-1}$)	0.03 ± 0.01a	0.05 ± 0.01b	0.04 ± 0.01b	0.1 ± 0.01c	12.4[**]
TNCv (%)	10.3 ± 0.8 ns	9.7 ± 0.7 ns	9.5 ± 2.0 ns	11.5 ± 0.7 ns	1.9 ns
TNCr (%)	11.4 ± 1.7a	9.8 ± 1.9a	16.6 ± 3.1b	16.5 ± 3.7b	3.4[*]

ns, non-significant.

[a] Significant difference in NAR between species was evaluated using *F* test corresponding to species × time interaction.

[*] $p < 0.05$.

[**] $p < 0.01$.

[***] $p < 0.001$.

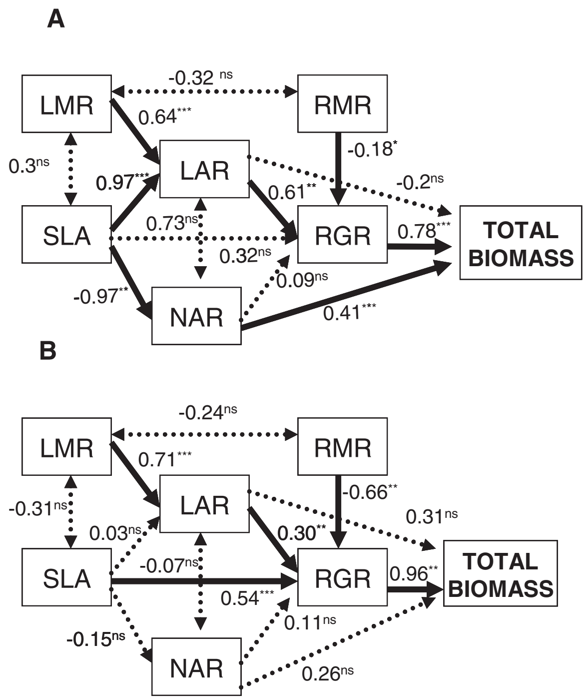


Fig. 2. Path diagrams for years 1 (A) and 2 (B), showing the direct and indirect effects of morphological (LAR, leaf area ratio; SLA, specific leaf area; LMR, leaf mass ratio; RMR, root mass ratio) and physiological (NAR, net assimilation rate) traits related with relative growth rate (RGR), on total biomass. Numbers indicate the direct β path coefficient between attributes. Asterisks indicate significance of the coefficient. $^{***}p < 0.001$; $^{**}p < 0.01$; and $^{*}p < 0.05$.

between SLA and total biomass) than the effects through LAR. Overall, species with low SLA showed less total biomass (Fig. 2A). The trade-off between leaf (LMR) and root (RMR) allocation was not significant, but allocation to roots explained the differential growth capacity between species: higher allocation to root was linked with lower RGR and total biomass (Fig. 2A and B).

Growth strategy plasticity

We found differences in growth capacity and allocation to reproduction between years. These differences were linked to changes in NAR, RMR, TNC, and harvest index that could be, in part, the result of the contrasting environmental conditions in the two years.

Plasticity of these key traits was not the same for annuals and perennial (significant interaction between species × year, see Table 2); and we tested year effects for each species separately. Perennials had a significant decrease in NAR ($F = 3.5^{*}$ and $F = 4.2^{*}$, for *P. pinetorum* and *P. mendocina*, respectively) and an increase in root allocation ($F = 2.9^{*}$ and $F = 4.8^{**}$, for *P. pinetorum* and *P. mendocina*, respectively) in the dry and cold year, while in annuals these traits were stable between years. In the year 2 (dry and cold conditions) TNC concentration in perennials during pre-anthesis was 49% less in relation to year 1 ($F = 5.2^{**}$ and $F = 6.3^{**}$, for *P. pinetorum* and *P. mendocina*, respectively). In annuals the storage capacity was not as plastic as that of perennials. Harvest index increased in year 2 in annual species ($F = 4.1^{**}$ and $F = 5.9^{**}$, for *P. gracilis* and *P. angustifolia*, respectively; Table 3) and was stable in perennials.

Discussion

In this study, we examined variations in the suites of traits related to growth capacity and carbon use strategy (*sensu* Grime, 1979; Craine, 2009) in congeneric annual and perennial *Physaria* species, in order to understand their association to the plant's life-cycle. Within perennial species, differences in carbon partitioning had been detected previously (González-Paleo and Ravetta, 2011; Masnatta and Ravetta, 2011). Specifically, allocation to reserves (that favors survival and persistence) and seed output seemed to be uncoupled. Within this context, we predicted that even when they maintained their perennial cycle, perennial *Physaria* would differ in the suite of traits determining C acquisition, which in turn are key determinants of plant productivity.

The four species of *Physaria* evaluated in our experiment differed in their relative growth rate and allocation to reproduction. At both extremes of RGR, we found a fast-growing, and high-yielding annual (*P. gracilis*), and a slow-growing, low-yielding perennial (*P. mendocina*). However, we found that these differences in RGR and reproductive biomass could not be fully linked to the plant's life-cycle.

In year 1, *P. angustifolia* and *P. pinetorum* had a growth rate opposite to our prediction based on life-cycle, supporting the hypothesis of uncoupled relationships between growth, C acquisition strategies and life-cycle.

Relative growth rate was high for the perennial and low for the annual, and the allocation to reproductive structures of the perennial *P. pinetorum* did not differ from that of annuals. Under the drier and cooler experimental conditions of the second year, both species showed intermediate values of RGR, reproductive biomass and harvest index compared to *P. gracilis* and *P. mendocina* (Tables 1 and 3). Although most plant growth studies have described differences between fast- and slow-growth strategies, there is only one case-study in which annual and perennial co-generic species with intermediate RGR have been reported (*Ehrharta* spp., Poaceae; Verboom et al., 2004). Still in this study the response was not fully characterized in terms of biomass allocation, leaf architecture and physiology, as determinants of growth rate.

The interspecific variation in morpho-physiological traits and RGR found in *Physaria* can be understood as arising from several contrasting carbon acquisition and use capacities, which are not determined by the life-cycle of species. To persist in time under regimes of nutrient limitation, plants have developed two main sets of adaptations: they optimize nutrient acquisition and/or reduce

Table 3
Generative traits for annual (*P. gracilis* and *P. angustifolia*) and perennial (*P. pinetorum* and *P. mendocina*) species of *Physaria* for: (A) year 1 and (B) year 2. Differences among species were evaluated for each year separately, due to significant species × year interactions for all traits ($p < 0.05$, not shown). Data are means ± S.E ($n = 6$).

(A) Year 1	*P. gracilis*	*P. angustifolia*	*P. pinetorum*	*P. mendocina*	*F* test
Reproductive biomass (g)	12.7 ± 1.4b	11.2 ± 3.0b	9.7 ± 1.1b	3.7 ± 0.7a	5.5^{**}
Harvest index (%)	52 ± 3b	46 ± 5b	50 ± 4b	32 ± 3a	3.1^{*}
(B) Year 2					
Reproductive biomass (g)	5.0 ± 1.0c	2.4 ± 0.4b	1.8 ± 0.5b	0.9 ± 0.1a	9.4^{***}
Harvest index (%)	62 ± 1b	36 ± 3ab	47 ± 2ab	26 ± 4a	4.2^{**}

ns, non-significant.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

nutrient losses. These adaptations are part of a well-known trade-off between resource acquisition and conservation (Grime, 1979; Berendse and Aerts, 1987; Aerts, 1990; Wright et al., 2004). Another potential cause of difference among this group of species is the effect of minor ambient clues in the environments from which these species are native to. While mean temperatures and precipitation were similar, unaccounted environmental differences could result in evolutionary history differences that may, in part, be responsible of the response gradient that we found.

The sets of traits present in *P. gracilis* and in *P. mendocina* are extremes in the C acquisition–conservation trade-off axis. The species with a fast-growth strategy and high biomass production, *P. gracilis*, was consistent to that reported for other annual species (Garnier, 1992; Ploschuk et al., 2005; Roumet et al., 2005; James, 2008). Concomitantly, *P. gracilis* showed a set of traits linked to a high resource acquisition capacity that include: large allocation to leaves (LMR and LAR) and reproduction; high SLA leaves; high leaf turnover rate (low leaf longevity); low root and storage allocation (Tables 2 and 3). In contrast and at the opposite extreme in this study, *P. mendocina* displayed a slow-growth strategy, defined by a set of traits associated with the protection of acquired resources. These traits included: low allocation to leaves and reproduction, low leaf turnover rateck, and especially low SLA and high allocation to roots and storage (Tables 2 and 3), all traits found in other perennials (Chapin, 1980; Roumet et al., 2005; Vilela et al., 2008).

The two remaining species, *P. angustifolia* and *P. pinetorum*, had intermediate growth rates between *P. gracilis* and *P. mendocina*. Their growth strategy can be viewed in two different ways depending on the set of characters to be considered. Carbon acquisition traits (LMR, LAR and SLA) for the annual *P. angustifolia* were those typically found in perennials, while for the perennial *P. pinetorum* these traits showed values typically found in annuals (Lambers et al., 1998). Thus, if carbon acquisition traits are considered, the growth strategy of these two species was opposite to what could be expected by their life cycle. However, if traits that frequently are overlooked in the determination of RGR, such as the storage capacity (RMR and TNC) and leaf longevity are considered in the characterization of the growth strategy, we found them to be in accordance with what is expected by their life cycle. This is the perennial had a larger investment in reserves and longer-lived leaves than the annual. Taken together both sets of traits (those involved in carbon acquisition and in carbon storage), help to explain the intermediate RGRs we found in *P. angustifolia* and *P. pinetorum* (Table 2).

The four *Physaria* species used in this study are native to areas in which severe water deficits limit biomass production (Rollins and Shaw, 1973). The above-described differences in carbon acquisition and use strategies and growth may allow them to cope with drought in different ways since drought tolerance depends on differences in functional traits, such as SLA, leaf longevity, below-ground biomass and plant longevity (Liu et al., 2012; Nippert et al., 2009). The suite of morphological traits of *P. gracilis* would allow it an opportunistic resource acquisition to speed up the completion of its life-cycle, before the onset of physiological water deficit. Annuals combine short life-cycles with high rates of growth, and maximize the use of resources while moisture in the soil lasts, in an escape strategy that relies on successful reproduction before the onset of severe stress (Mooney et al., 1987; Golluscio and Sala, 1993). However, species with this strategy may not be able to off-set the potential disadvantage of water loss from a large leaf area development. Thus, under longer periods of drought, plant survival could be compromised before successful reproduction (Preston and Ackerly, 2003).

Conversely, the slow-growth strategy found in the perennial *P. mendocina* was determined by traits linked to a dehydration avoidance strategy (Table 2). One of the mechanisms to reduce water losses is to produce sclerophyllous leaves (small, thick leaves with low SLA; Poorter et al., 2009). This leaf trait also provides herbivory resistance, tissue longevity, and tight nutrient recycling (Aerts, 1999; Fraser and Grime, 1999). Water uptake is maximized by adjusting the allocation pattern, making the roots and storage higher hierarchical sinks (Lynch, 1995; Comas et al., 2013).

The intermediate growth strategy found in the perennial *P. pinetorum* appears to combine the advantage of an opportunistic resource acquisition (found also in the annual *P. gracilis*) that provides a fast growth when resources are available, and the benefits of intermediate values of SLA in drought-prone environments. Specific leaf area has been shown to be strongly linked to drought-tolerance and appears as a key character for carbon acquisition and growth rate (Garnier, 1992; Reich, 1993), and has already been highlighted as a key functional marker of plant strategies (Garnier et al., 2001). However, we did not find a clear relationship between leaf morphology and functioning, as expected according to leaf economic spectrum (Wright et al., 2004). High SLA did not always translate into high CO_2 assimilation rate per unit of leaf area. These contradictory results indicate that the patterns of leaf structure and functions may be not as universal as previously thought, and at least in some cases is species–specific. The choice of dimensions in which to express leaf traits and/or process is a controversial issue (Poorter et al., 2014). It has been proposed that the decoupling of photosynthetic characteristics from other leaf traits such as SLA is related to how photosynthetic rate is normalized (i.e., mass-basis or area basis). When parameters are expressed per unit dry mass, photosynthetic rate scales positively with SLA (Westoby et al., 2013). However, Osnas et al. (2013) and Lloyd et al. (2013) attribute the significance of this relationship to the existence of "spurious" correlations as consequence of using SLA as factor for normalization, and proposed that leaf area based photosynthesis is the logical basis for the expression of this trait.

Changes in the availability of any resource trigger changes in functional traits that modulate the ability of plants to acquire or conserve the resource (Chapin et al., 1993). In particular, resource-acquisitive species are presumed to have greater plasticity of functional traits to maintain growth than resource-conservative species (Crick and Grime, 1987; Grassein et al., 2010). Our results suggest that plasticity in functional traits which determine growth capacity in pre-anthesis are more strongly linked to the plant's life-cycle, and not to the carbon use strategy. Biomass and RGR where much more plastic in perennials than in annuals. Traits such as NAR, RMR, and TNC followed the same pattern. This plasticity is of key relevance in environments prone to frost and prolonged winters followed by periods in which plants can grow but with low temperatures and limited carbon assimilation (Tursun et al., 2011). On the other side, annuals were more plastic in reproductive traits than perennials, increasing the proportion of biomass allocated to reproductive structures in the colder and drier year, which agrees with their strategy to maximize productivity (Vilela and González-Paleo, 2015).

On the other hand, this screening study is performed just beginning on the emerging use of *Physaria* as an oilseed crop. Characterization of biomass models in this genus is underway to determine non-adaptive traits correlated with increasing productivity in improved cultivars. The understanding of the mechanisms responsible for carbon use and biomass production in annual and perennial herbs is not only relevant because survival and reproduction depend on plant size and therefore on growth rate (Shipley, 2006). There is a current debate on the possibility of developing new perennial crops for sustainable agricultural systems (Pimentel et al., 2012). Still, since perennials tend to have lower RGR and produce less biomass and seeds than their annual counterparts (Obeso, 2002) they tend to be discarded when new crops are developed. Understanding the mechanisms behind resource use and growth of annuals and perennials can help both in the selection of functional types and the design of cultivation technology. For example, our data show differences in the strategy used for carbon gain by *P. mendocina* and *P. gracilis*. They represent alternative functional types for environments that differ in resource availability. On one side, the perennial *P. mendocina* with conservative strategy for C acquisition may offer benefits as a perennial crop that buffers biomass and seed production in years of low availability of water and nutrients, but sacrifices the fast biomass production when resources are abundant. Conversely, *P. gracilis* that exhibits characters that support a high growth rate, may be highly responsive to infrequent periods of high resource availability, but have a low tolerance to low resource availability. The result would be a significant variation in biomass and seed production between years. The intermediate carbon use strategy of *P. angustifolia* and *P. pinetorum* combines moderate biomass production with an intermediate capacity for buffering the decrease in productivity in drought-prone environments.

Acknowledgement

This work was supported by CONICET, PIP 112-200801-03142. The main author held a scholarship from CONICET during the time of these experiments was done.

References

Aerts, R., 1990. Nutrient use efficiency in evergreen and deciduous species from heathlands. Oecologia 84, 391–397.

Aerts, R., 1999. Interspecific competition in natural plant communities: mechanisms, trade-offs and plant–soil feedbacks. J. Exp. Bot. 50, 29–37.

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

Arendt, J.D., 1997. Adaptive intrinsic growth rates: an interpretation across taxa. Q. Rev. Biol. 72, 149–177.

Benech Arnold, R.L., Fenner, M., Edwards, P.J., 1992. Mineral allocation to reproduction in *Sorgum bicolor* and *Sorgum halpense* in relation to parental nutrient supply. Oecologia 92, 138–144.

Berendse, F., Aerts, R., 1987. Nitrogen-use-efficiency: a biologically meaningful definition? Funct. Ecol. 1, 293–296.

Brahim, K., Ray, D., Dierig, D., 1998. Growth and yield characteristics of *Lesquerella fendleri* as a function of plant density. Ind. Crops Prod. 9, 63–71.

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

Canham, C.D., Kobe, R.K., Latty, E.F., Chazdon, R.L., 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. Oecologia 121, 1–11.

Chapin, F.S., 1980. The mineral nutrition of wild plants. Annu. Rev. Ecol. Evol. Syst. 11, 233–260.

Chapin, F.S., Autumn, K., Pugnaire, F., 1993. Evolution of suites of traits in response to environmental stress. Am. Nat. 142, 78–92.

Coleman, J.S., McConnaughay, K.D.M., Ackerly, D.D., 1994. Interpreting phenotypic variation in plants. Trends Ecol. Evol. 9, 187–191.

Comas, L.H., Becker, S.R., Cruz, V.M.V., Byrne, P.F., Dierig, D.A., 2013. Root traits contributing to plant productivity under drought. Front. Plant Sci. 4, 1–16.

Crick, J.C., Grime, J.P., 1987. Morphological plasticity and mineral nutrient capture in two herbaceous species of contrasted ecology. New Phytol. 107, 403–417.

Craine, J., 2009. Resource Strategies of Wild Plants. Princeton University Press.

DeHaan, L.R., Van Tassel, D.L., 2014. Useful insights from evolutionary biology for developing perennial grain crops. Am. J. Bot. 101, 1801–1819.

DeHaan, L.R., Van Tassel, D.L., Cox, T.S., 2005. Perennial grain crops: a synthesis of ecology and plant breeding. Renew. Agric. Food. Syst. 20, 5–14.

Dierig, D.A., Thompson, A.E., Nakayama, F., 1993. *Lesquerella* commercialization efforts in the United States. Ind. Crops Prod. 1, 289–293.

Fraser, L.H., Grime, J.P., 1999. Interacting effects of herbivory and fertility on a synthesized plant community. J. Ecol. 87, 514–525.

Garnier, E., 1992. Growth analysis of congeneric annual and perennial grass species. J. Ecol. 80, 665–675.

Garnier, E., Laurent, G., 1994. Leaf anatomy, specific mass and water content in congeneric annual and perennial grass species. New Phytol. 128, 725–736.

Garnier, E., Shipley, B., Roumet, C., Laurent, G., 2001. A standardized protocol for the determination of specific leaf area and leaf matter. Ecology 15, 688–695.

Golluscio, R.A., Sala, O.E., 1993. Plant functional types and ecological strategies in Patagonian forbs. J. Veg. Sci. 4, 839–846.

González-Paleo, L., 2010. Cambios en atributos eco-fisiológicos asociados a la supervivencia, la perennidad y la estabilidad del rendimiento, resultantes del incremento del rendimiento por selección en especies anuales y perennes de *Lesquerella* (Brassicacea). In: Thesis Doctoral. Universidad Buenos Aires-Facultad de Agronomía.

González-Paleo, L., Ravetta, D., 2011. Relationships between reproductive output, morpho-physiological traits and life span in *Lesquerella* (Brassicaceae). Ind. Crops Prod. 34, 1386–1392.

Grassein, F., Till-Bottraud, I., Lavorel, S., 2010. Plant resource-use strategies: the importance of phenotypic plasticity in response to a productivity gradient for two subalpine species. Ann. Bot. 106, 637–645.

Grime, J.P., 1979. Plant Strategies and Vegetation Processes. Wiley, Chichester, UK.

Grime, J.P., 2001. Plant Strategies, Vegetation Processes, and Ecosystem Properties. John Wiley & Sons, New York.

Grime, J.P., Hunt, R., 1975. Relative growth-rate: its range and adaptive significance in a local flora. J. Ecol. 63, 393–422.

Hautekeete, N., Piquot, Y., Van Dijk, H., 2001. Investment in survival and reproduction along a semelparity–iteroparity gradient in the *Beta* species complex. J. Evol. Biol. 14, 795–804.

Hautekeete, N.C., Van Dijk, H., Piquot, Y., Teriokhin, A., 2009. Evolutionary optimization of life-history traits in the beet *Beta vulgaris* subsp. *maritima*: comparing model to data. Acta Oecol. 35, 104–116.

Hunt, R., Causton, D.R., Shipley, B., Askew, A.P., 2002. A modern tool for classical plant growth analysis. Ann. Bot. 90, 485–488.

James, J.J., 2008. Effect of soil nitrogen stress on the relative growth rate of annual and perennial grasses in the intermountain west. Plant Soil 310, 201–210.

Lambers, H., Poorter, H., 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Adv. Ecol. Res. 23, 187–261.

Lambers, H., Chapin, F.S., Pons, T.L., 1998. Plant Physiological Ecology. Springer, New York.

Liu, Y., Pan, Q., Zheng, S., Ben, Y., Han, X., 2012. Intra-seasonal precipitation amount and pattern differentially affect primary production of two dominant species of Inner Mongolia grassland. Acta Oecol. 44, 2–10.

Lloyd, J., Bloomfield, K., Domingues, T.F., Farquhar, G.D., 2013. Photosynthetically relevant foliar traits correlating better on a mass vs an area basis: of ecophysiological relevance or just a case of mathematical imperatives and statistical quicksand? New Phytol. 199, 311–321.

Lynch, Y., 1995. Root architecture and plant productivity. Plant Physiol. 109, 7–13.

Marañon, T., Grubb, P.J., 1993. Physiological basis and ecological significance of the seed size and relative growth rate relationship in Mediterranean annuals. Funct. Ecol. 7, 591–599.

Masnatta, W.J., Ravetta, D., 2011. Seed-yield and yield components response to source–sink ratio in annual and perennial species of *Lesquerella* (Brassicaceae). Ind. Crops Prod. 34, 1393–1398.

Metcalf, C.J., Rees, M., Alexander, J.M., Rose, K., 2006. Growth–survival trade-offs and allometries in rosette-forming perennials. Funct. Ecol. 20, 217–225.

Meziane, D., Shipley, B., 1999. Interacting components of interspecific relative growth rate: constancy and change under differing conditions of light and nutrient supply. Funct. Ecol. 13, 611–622.

Mitchell, R.J., 1992. Testing evolutionary and ecological hypotheses using path analysis and structural equation modeling. Funct. Ecol. 6, 123–129.

Mooney, H.A., Ehleringer, J., Berry, J.A., 1987. High photosynthetic capacity of a winter annual in Death Valley. Science 194, 322–324.

Nippert, J.B., Fay, P.A., Carlisle, J.D., Knapp, A.K., Smith, M.D., 2009. Ecophysiological responses of two dominant grasses to altered temperature and precipitation regimes. Acta Oecol. 35, 400–408.

Obeso, J.R., 2002. The cost of reproduction in plants. New Phytol. 155, 321–348.

Osnas, J.L., Lichstein, J.W., Reich, P.B., Pacala, S.W., 2013. Global leaf trait relationships: mass, area, and the leaf economics spectrum. Science 340, 741–744.

Patty, L., Halloy, S.R.P., Hiltbrunner, E., Körner, C., 2010. Biomass allocation in herbaceous plants under grazing impact in the high semi-arid Andes. Flora 205, 695–703.

Pimentel, D., Cerasale, D., Stanley, R.C., Perlman, R., Newman, E.M., Brent, L.C., Mullan, A., et al., 2012. Annual vs perennial grain production. Agric. Ecosyst. Environ. 161, 1–9.

Pino, J., Sans, F.X., Masalles, R.M., 2002. Size-dependent reproductive pattern and short term reproductive cost in *Rumex obtusifolia* L. Acta Oecol. 23, 321–328.

Ploschuck, E.L., Windauer, L., Ravetta, D., 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. J. Arid Environ. 47, 373–386.

Ploschuk, E.L., Slafer, G.A., Ravetta, D.A., 2005. Reproductive allocation of biomass and nitrogen in annual and perennial *Lesquerella* crops. Ann. Bot. 96, 127–135.

Poorter, H., Bongers, F., 2006. Leaf traits are good predictors of plant performance across 53 rain forest species. Ecology 87, 1733–1743.

Poorter, H., Lewis, C., 1986. Testing differences in relative growth rate: a method avoiding curve fitting and pairing. Physiol. Plant 67, 223–226.

Poorter, H., Niinements, Ü., Poorter, L., Wright, I.J., Villar, R., 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytol. 182, 565–588.

Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P., Mommer, L., 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol. 193, 30–50.

Poorter, H., Lambers, H., Evans, J.R., 2014. Trait correlation networks: a whole-plant perspective on the recently criticized leaf economic spectrum. New Phytol. 201, 378–382.

Preston, K.A., Ackerly, D.D., 2003. Hydraulic architecture and the evolution of shoot allometry in contrasting climates. Am. J. Bot. 90, 1502–1512.

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

Reich, P.B., 1993. Reconciling apparent discrepancies among studies relating life-span, structure and function of leaves in contrasting plant life forms and climates: the blind men and the elephant retold. Funct. Ecol. 7, 721–725.

Reich, P.B., Ellsworth, D.S., Walters, M.B., 1998. Leaf structure (specific leaf area) modulates photosynthesis–nitrogen relations: evidence from within and across species and functional groups. Funct. Ecol. 12, 948–958.

Rollins, R.C., Shaw, E.A., 1973. The Genus *Lesquerella* (Crucifereae) in North America. Harvard University Press, Cambridge, Massachusetts.

Roumet, C., Urcelay, C., Díaz, S., 2005. Suites of root traits differ between annual and perennial species growing in the field. New Phytol. 170, 357–368.

Shipley, B., 2002. Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: relationship with daily irradiance. Funct. Ecol. 16, 682–689.

Shipley, B., 2006. Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: relationships with daily irradiance. Funct. Ecol. 16, 1–10.

Shipley, B., Meziane, D., 2002. The balanced growth hypothesis and the allometry of leaf and root biomass allocation. Funct. Ecol. 16, 326–331.

Tilman, D., 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton.

Tursun, N., Seyithanoglu, M., Uygur, F.N., Elibuyuk, I.O., Elibuyuk, E.A., 2011. Seasonal dynamics of soluble carbohydrates in rhizomes of *Phragmites australis* and *Typha latifolia*. Flora 206, 731–735.

Verboom, G.A., Linder, H.P., Stock, W.D., 2004. Testing the adaptive nature of radiation: growth form and life history divergence in the African grass genus *Ehrharta* (Poaceae: Ehrhartoideae). Am. J. Bot. 91, 1364–1370.

Vilela, A.E., González-Paleo, L., 2015. Changes in resource-use strategy and phenotypic plasticity associated with selection for yield in wild species native to arid environments. J. Arid Environ. 113, 51–58.

Vilela, A., Cariaga, R., González-Paleo, L., Ravetta, D.A., 2008. Trade-offs between reproductive allocation and storage in species of *Oenothera* L. (Onagraceae) native to Argentina. Acta Oecol. 33, 85–92.

Weiner, J., 2004. Allocation, plasticity, and allometry in plants. Perspect. Plant Ecol. Evol. Syst. 6, 207–215.

Westoby, M., 1998. A leaf–height–seed (LHS) plant ecology strategy scheme. Plant Soil 199, 213–227.

Westoby, M., Reich, P.B., Wright, I.J., 2013. Understanding ecological variation across species: area-based vs mass-based expression of leaf traits. New Phytol. 199, 322–332.

Wright, I.J., Reich, P.B., Westoby, M., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827.

Yemm, E.W., Willis, A., 1954. The estimation of carbohydrates in plant extracts by anthrone. Biochem. J. 57, 508–514.