



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



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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.

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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 (Marañón 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).

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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 $\mu\text{mol m}^{-2} \text{s}^{-1}$). 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),

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