



## Back to perennials: Does selection enhance tradeoffs between yield and longevity?



Luciana González-Paleo\*, Alejandra Elena Vilela, Damián Andrés Ravetta

CONICET-Museo Egidio Feruglio, Fontana 140, Trelew, Chubut, Patagonia, Argentina

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### ABSTRACT

Perennial plants allocate more resources belowground and have longer-lived leaves than their annual counterparts, which are the basis for the promotion of perennial crops towards a more sustainable agriculture. On the downside, perennial plants selected for high seed-yield might show tradeoffs between current reproduction and long-term reproduction or survival, raising the questions of whether this high yield can be sustained over time and whether such tradeoffs can be overcome through selection. We compared growth, reproduction and the storage of reserves, over 3 years in wild and high-yielding accessions of *Physaria mendocina*. We found evidence of a tradeoff between current and future reproduction, responsible for a decrease in yield with age, in selected accessions. Selected accession had 76% more accumulated seed-yield in relation to wild accessions, but they also concentrated seed-yield and had an enhanced harvest index in the first year. Wild accessions maintained seed production over time. Resources allocated to reproduction were limited for both root allocation and carbohydrate accumulation after the second year. Wild and selected accessions consumed half of their storage carbon during reproduction, but replenishment of storage organs was 60% lower in selected accession compared to wild ones. This response could be related to a lower recovery of the root system after senescence. Empirical information about the pattern of use of reserves and their relationships with the ontogenetic changes in leaf functioning and root architecture is crucial when defining new criteria of selection of perennial species, since they will influence longevity and yield stability.

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### 1. Introduction

Agricultural systems around the world are facing a renewed demand to improve sustainability. Traditional systems relying on annual crops have substantial negative impacts on ecosystem functions (i.e. nutrient cycling, water quality and carbon emissions; Pimentel et al., 2012), leading to changes in dryland salinity, soil erosion and degradation, and nutrient leaching (Tilman et al., 2011; Pimentel et al., 2012). These problems can be reduced through the reintroduction in agricultural systems of productive and profitable perennial plants because they more closely mimic the original vegetation (Jackson, 2002; Ridley and Pannell, 2005; Cox et al., 2006; DeHaan et al., 2005; González-Paleo and Ravetta, 2015). Perennials have deep long-lived roots with a greater carbon storage capacity than annuals. This deep root facilitates water infiltration, reduces soil erosion risks, and maintains more soil carbon compared with annual crops (Glover and Reganold, 2010). Leaf tissues of perennials are usually more lignified to increase leaf persistence, tolerate

herbivory and resist environmental stress. Plants with long-lived leaves are more efficient in water and nutrients utilization (Wright et al., 2004), and need less fertilization because they can reutilize nutrients in following years.

In spite of this potential increased sustainability of perennial grain crop systems compared to that of traditional annual systems, the existence of tradeoffs between longevity and seed-yield still constitutes a major obstacle for extensive cultivation of perennials (Wagoner, 1990; Pimm, 1997; DeHaan et al., 2005). One potential approach to develop high-yielding perennial crops involves the conversion of promising wild perennials species into crops (Cox et al., 2002). In this case, the candidate is already perennial, but lacks most of the characteristics that would make it a good crop, and therefore, it needs to be selected for desirable agronomic traits, such as high seed production and harvest index, reduced fruit dehiscence, etc. (DeHaan et al., 2016). The challenge of breeding programs is to maintain those traits associated to the perennial habit (i.e. root system, storage capacity, leaf longevity, among others) while increasing yield and maintaining it stable for several years (Cox et al., 1985; Glover and Reganold, 2010; Vico et al., 2015).

Perennial species which have been selected for increased seed-yield usually show the cost of reproduction in terms of growth (i.e.

\* Corresponding author.

E-mail address: [lgonzalezpaleo@mef.org.ar](mailto:lgonzalezpaleo@mef.org.ar) (L. González-Paleo).

reduced biomass production), sustained reproduction (i.e. lower seed-yield or number of fruits as years of cultivation progress), or survival (lower storage capacity; Piper and Kulakow, 1994; Aragón et al., 2009) in subsequent years. In spite of a general agreement in the ecological literature over the existence of trade-offs between current reproduction and future plant performance, empirical results are inconsistent. Some studies describe negative effects of current reproduction on future performance, while others fail to detect these negative effects (Obeso, 2002; Piper, 1993; Reekie and Avila-Sakar, 2005; Van Dijk, 2009). Plant breeders have pointed out that these physiological tradeoffs do not necessarily limit productivity of perennials because long-lived plants intercept more sunlight over the course of a year than their annual counterparts (e.g. Glover et al., 2010) or have an instantaneous net CO<sub>2</sub> uptake higher than co-generic annuals (Jaikumar et al., 2013). Therefore, at least some perennials appear to have enough total carbon available both for current reproduction and future performance. Even if these tradeoffs exist, crops can potentially be selected simultaneously for traits that increase seed-yield while maintaining plant longevity (Jackson and Dewald, 1994; DeHaan et al., 2005; DeHaan and Van Tassel, 2014).

Because of these functional uncertainties, there is a clear need for insight into the indirect changes provoked by selection for high yield on plants' future performance (growth, reproduction and survival), in order to identify additional selection criteria for wild perennials. Here we focused on two questions: Does increased yield have indirect costs on future growth, reproduction or longevity? Is the increased yield of selected perennial plants stable over time? We compared growth, reproduction and storage over time in wild and high-yield selected accessions of *Physaria mendocina* (Phil) Kurtz (Brassicaceae) to test the following hypotheses:

- 1) Selection for high seed-yield will provoke tradeoffs between current and future reproduction. We predict that reproduction (seed yield and yield components) will be maximum during the first year and will decrease with age (i.e. instability of yield) in selected accessions, while allocation to reproduction will be lower and more stable over time in wild plants.
- 2) Selection for high-yield will provoke tradeoffs between current reproduction and future growth. We predict that growth will be maximum during the first year and will decrease with age in selected accessions, while these traits will be more stable over time in wild plants.
- 3) Selection for high seed-yield will change the pattern of accumulation of total non-structural carbohydrates (TNC). We predict that wild accession will show a full recovery of root TNC levels after each reproductive event, while the regain of stores in high-yield accessions will be incomplete, leading to a decrease of the pool of TNC with age (i.e. tradeoffs between reproduction and longevity).

## 2. Materials and methods

### 2.1. Plant material and experimental design

*Physaria mendocina* (Brassicaceae) is a perennial forb, native to the Monte desert in Argentina. It forms an acaulescent rosette that develops elongate stems (bolting) bearing leaves, flowers and capsules during spring and early summer. The end of the reproductive period occurs in late January (González-Paleo and Ravetta, 2012). Plants reach 15–30 cm in height and produce many stems. Seeds are contained in pea-sized, bladder-like pods along the stem. The seed size is smaller than alfalfa and most clover species. All *Physaria* species evaluated so far are self-incompatible and cross pollinated (Dierig and Ray, 2008). This species, as well as other species within

the genus *Physaria* have been proposed as potential new seed-oil crops for drylands, with mediterranean-type climates (Dierig et al., 1993). In particular *P. mendocina* exhibits a conservative resource-use strategy that might contribute to increased ecological and economical sustainability in low-resource environments (Ravetta and Soriano, 1998; González-Paleo and Ravetta, 2011, 2015; Pastor-Pastor et al., 2015). *Physaria* seeds contain hydroxy fatty-acids, similar to those of castor oil (lesquerolic, auricollic and densipolic acids; Dierig et al., 1993). Large markets exist for these chemical feedstocks for lithium greases, polymers in paints and coatings, base stocks for lubricants, nylon, hydraulic fluids, and applications in the personal care industry. The hydroxyl group of these oils makes it a prime candidate as additive to diesel fuel to improve lubricity (Naughton, 1992).

A field experiment was carried out in Patagonia, Argentina (43°81'70"iS; 65° 82'90"iW). We compared wild and high-yield selected accessions in a completely randomized design. Seedlings of the wild accession came from seed collected from a native stand at Lihue-Calel, La Pampa, Argentina and multiplied in Chubut. This same wild accession was the source of base germplasm to generate the selected accession through mass selection (González-Paleo and Ravetta, 2012). The selection criterium was individual plant seed yield (bulk seeds of three top yielding plants). This criterium was applied to plants growing in stands of 160 plants per species, in introductory gardens in the Chubut River Valley. The selection cycle was carried on for three generations (González-Paleo and Ravetta, 2011).

Seeds of both groups were sown in the fall, in germination trays filled with soil: peat moss (1:1 by volume). Seedlings were transplanted to the field 66 days after sowing in a completely randomized experiment comparing selected types to wild types. Experimental units consisted in plots (2 m wide × 1.5 m long) with a density of 10 plants m<sup>-2</sup>, with 0.17 m between plants. Rows were 0.4 m apart. Each plot had 32 plants, 10 reps per selection level, for a total of 320 plants per selection level. Plots were flood irrigated every 20–25 days until field capacity. Weeds were removed manually. Fungal controls with etilen bis ditiocarbamate-zinc (zineb, 2 g/l) and 2-metoxicarbamoil-bencimidazol (carbendazim, 0.5 cm<sup>3</sup>/l) were applied monthly.

### 2.2. Plant measurements

During three years, plants were harvested at three phenological stages: (1) rosette: vegetative stage before bolting; (2) anthesis: 50% of floral stems of a plant bear at least one flower; (3) maturity: 50% of floral stems of a plant bear at least one mature pod with dark and hard seeds.

We compared the dynamics of growth and reproduction of selected types and wild plants over three years. We used dry total biomass and leaf dry biomass as a proxy for growth (Poorter et al., 2009) and seed-yield and yield components as proxies for reproduction (Violle et al., 2007). Root allocation (dry mass) and carbohydrates reserves were used as a fitness proxy for survival and plant longevity (Kobe, 1997; Vilela and González-Paleo, 2015). We also compared the dynamics of reserves accumulation and use over time between wild and selected accessions.

For allocation analysis, individual plants (10 reps per selection group; 1 plant per plot) were separated into roots, leaves, and reproductive structures, and placed in an oven at 60°C until weight constancy, and weighed. Total biomass included roots that were sampled using a core of similar diameter of the above-ground rosette. Seed-yield was determined at maturity (10 reps per selection group; 1 plant per plot). We counted the number of fruits per plant and the number of seeds per fruit. Individual seed-weight was estimated using sub-samples of 100 seeds. Harvest index (HI) was

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