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Age-related changes in nitrogen resorption and use efficiency in the perennial new crop *Physaria mendocina* (Brassicaceae)

Alejandro Pastor-Pastor[a,*], Luciana González-Paleo[b], Alejandra Vilela[b], Damián Ravetta[b]

[a] *Museo Paleontológico Egidio Feruglio FONCyT, Av. Fontana 140, Argentina*
[b] *Museo Paleontológico Egidio Feruglio CONICET, Av. Fontana 140, Argentina*

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ABSTRACT

Domestication of desert-adapted species and their development into perennial crops has been proposed as an alternative to increase cropping intensity in arid lands, while reducing nitrogen inputs and losses. Among traits involved in nitrogen conservation much attention has been drawn to resorption patterns. However, understanding of intra-population variability in resorption and nitrogen use efficiency is required prior to the development of new crops. Here we evaluate age-related changes in resorption patterns and nitrogen use efficiency (NUE) within a wild population of *Physaria mendocina* (Brassicaceae). We generated a relative age index, based on morphological traits, and we use it as an independent variable to regress nitrogen concentrations in roots and leaves (green and senesced), nitrogen resorption efficiency and use efficiency. Nitrogen in green and senesced leaves decrease with age, resorption efficiency did not change, and nitrogen use efficiency increased. The lower nitrogen concentration in green leaves and higher proficiency (lower nitrogen concentrations in senesced leaves) of older plants might be due to a decrease in acquisition capacity. Constant efficiency is explained by the lack of differences in concentration in green and senesced leaves slopes. Higher proficiency in older plants resulted in higher NUE; this relationship would be modulated by nitrogen concentration in green leaves, which, in turn, is controlled by nitrogen availability and acquisition. These findings have implications in the domestication process, since in perennial species biomass production and internal plant nitrogen turnover over multiple seasons, are central key to physiological functions such as plant re-growth and winter survival. We identified a few questions as directions for future research.

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1. Introduction

In arid ecosystems nitrogen availability is one of the main restrictions for plant growth and, hence, for agronomical production (González-Dugo et al., 2010; Anfinrud et al., 2013). Domestication of desert-adapted species and their development into perennial crops has been proposed as alternative to increase cropping intensity in arid lands while reducing nitrogen requirements and losses (Ravetta and Soriano, 1998; Crews, 2005; Asbjornsen et al., 2014). Perennial xerophytes exhibit a suite of traits such as low relative growth rate, leaves with low nitrogen content, small specific leaf area and effective nutrient resorption that contribute to a low dependence on outer sources and small losses of nitrogen (Aerts, 1996; Aerts and Chapin, 2000; Wright et al., 2002). Among traits involved in nitrogen conservation much attention has been drawn to resorption patterns, because it allows leaf nitrogen to be reused rather than lost with leaf-fall (Aerts, 1996; Killingbeck, 1996; Aerts and Chapin, 2000). Resorption can be measured as the proportion of nitrogen resorbed from senesced leaves (resorption efficiency or NRE) or as the nitrogen concentration in senesced leaves (resorption proficiency; Killingbeck, 1996). Both characteristics determine leaf-level nitrogen use efficiency (NUE; Eckstein et al., 1999). Both resorption efficiency and proficiency vary with a large number of variables (Kobe et al., 2005; Yuan and Chen, 2009).

Most studies on resorption and NUE in natural populations and crops do not consider intra-population variability (Yuan et al., 2004). Differences in age or size among individuals might provoke a significant variability in plant structure and functioning (Callaghan 1980; Groom et al., 1997; McConnaughay and Coleman, 1999). For instance, leaves of young plants tend to contain more nitrogen that allow for higher photosynthetic rates (Niinemets, 2004) and are closer to an acquisitive strategy in the use of nutrients than leaves of mature individuals (Mediavilla et al., 2013). Also, resorption might

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* Corresponding author. Tel.: +54 280 443 2100; fax: +54 2965 432100.
E-mail address: apastor@mef.org.ar (A. Pastor-Pastor).

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be affected by the age of the plant (Landsberg and Gower, 1997; Yuan and Chen, 2010) and its importance increases when nitrogen uptake is limited (Gower et al., 1996; Wright and Westoby, 2003). At the same time, NUE is influenced by plant size (Yuan et al., 2004).

The understanding of nitrogen use efficiency and resorption patterns is required prior to the election of crop ideotypes, and central to the plant selection process aimed to increase yield without a massive intensification in resource inputs. The description of intra-population variability of these traits in wild plants is a relevant step in their domestication process since it provides basic knowledge to propose new selection criteria to improve plant performance without discarding nitrogen conservation strategies (Dawson et al., 2008; Weih et al., 2011).

Here, we evaluate intra-population variability in nitrogen resorption and leaf-level NUE in a wild population of *Physaria mendocina* (Phil.) Kurt (Brasicasseae), a species that is being developed as a new oil-seed crop for irrigated valleys in Patagonia, Argentina and similar cold arid environments (González-Paleo and Ravetta, 2011).

Intra-population variability in resorption and NUE may be a consequence of differences among individuals in age, size, or both. Usually, age and size are correlated (Bonser and Aarssen, 2001), but in wild populations micro-environmental variations might affect plant size, and therefore, it is not easy to determine the age of perennial herbs. Despite methodological difficulties, the knowledge of the age of an individual is crucial for understanding species fitness, regeneration potential and survival (Dhyani et al., 2012). Hence, we use here a relative-age index, based on qualitative and morphological traits. These traits have been utilized in previous studies to determine the age of perennial plants and to evaluate physiological changes throughout the life cycle (Jørgensen and Olesen, 2000; Niinemets, 2004, 2005; Dhyani et al., 2012). Indexes of relative-age are often based on the whole plant size or the size of specific parts of the plant, such as rhizomes (Niinemets, 2004, 2005) or shoot diameter (Schweingruber and Poschlod, 2005). Although a relative-age index cannot be directly related to calendar age, its use is supported by the fact that responses to stress and plant role in community are controlled by ontogenetic state rather than by calendar age (Lewis et al., 2002; Weiner, 2004).

We addressed the following questions:

i. Does nitrogen use efficiency and resorption change with plant relative-age?
ii. Which factors explain differences in resorption and NUE between individuals of different relative-age?

Finally, we discuss the implications of our results for the process of domestication of perennial herbs.

2. Materials and methods

2.1. Study site and plant material

This study was carried out in a wild population of *P. mendocina* at Lihué Calel National Park, in the South center of La Pampa, Argentina (37°57'S, 65°33'W). In this area, the mean annual precipitation is 400 mm, the mean monthly temperature ranges between 7 °C in July and 24 °C in January, with a mean annual of 15 °C (Cinti, 1983; Mazzola et al., 2008). Soils in this area are poorly developed Mollisols with a petrocalcic horizon at 1 m deep and <3% content of organic matter and <0.15% of nitrogen (INTA, 1980). Native vegetation is a typical shrubland of the Monte phytogeographical region, dominated by *Larrea divaricata*, *Ligaria cuneifolia* and *Lonicera nitida*, *Prosopis alpataco*, *Monthea aphylla* and *Schinus fasciculatus* (Cabrera, 1994).

Physaria has been proposed as a potential new oil-seed crop for irrigated valleys in Patagonia (Argentina), because it contains high levels of hydroxy fatty acid and because it exhibits several morphological, physiological, and phenological traits that could contribute to increase ecological and economical sustainability in marginal environments (Ravetta and Soriano, 1998; Ploschuk et al., 2001; González-Paleo and Ravetta, 2011).

2.2. Plant sampling and relative-age determination

Plants of *P. mendocina* were harvested on the 20 October, 2013. Transects used in this study were the same used in Masnatta et al. (2012). A 300 × 300 m plot was defined in a well-preserved wild population. Within this plot three 48 × 72 m sub-plots were delimited and three transects were established in each plot. Transects were separated at least by 12 m. In each transect we set up nine 8 × 0.1 m. plots and we collected plants inside. Population density and structure are estimated in Masnatta et al. (2012). Plants were classified by sizes using visual criteria in three classes: (1) large (plant diameter >4 cm), (2) intermediate (1.5–4 cm) and (3) small (<1.5 cm), and were transported to the laboratory for morphological measurements. Plant diameter was measured as the mean value of two perpendicular diameters. Stem length was measured as the total longitude of the brachyblast. Root diameter was measured at the scar between the main stem and root, using a Vernier caliper. All three were positively correlated to total biomass ($P < 0.001$; data not shown). Senesced leaves of *P. mendocina* often remain on the brachyblast for at least two growth-seasons in different stages of senescence. We classified leaves into four different stages: (1) green leaves, (2) senesced leaves of the present year, (3) senesced leaves of previous years, and (4) scars or remnants left by leaves on the brachyblast. Leaves (2) and (3) were easily recognizable by the color (gray–brown vs grayish–black). We assigned to each individual plant the largest number, of leaf types present (i.e., a plant with leaves 1, 2 and 3, was classified as 3).

Plant diameter, root diameter, stems length and leaf types were combined to conduct a Principal Components Analysis (PCA; Fig. 1). The PCA gave only one Principal Component (PC1) with eigenvalues higher than 1, explaining 78.9% of the total variance (Table 1). All four traits were important structuring PC 1 (factor loading >0.80).

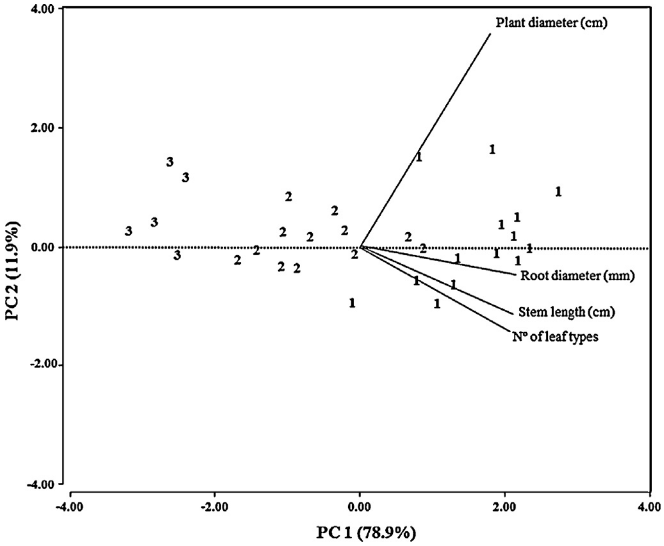

Fig. 1. Plant relative age index, from younger (left) to older (right) plants. The relative-age index is represented as a straight horizontal line (axis 1). Plant were labelled as classified by size in the field (3 for small and 1 for large plants). Individual plant scores were used in all subsequent analyses as a proxy for the whole plant relative age.

Table 1
Correlation matrix for Pearson's coefficients among all measured traits. N_{green}, nitrogen concentration in green leaves (mg/g^{-1}); $N_{senesced}$, nitrogen concentration in senescent leaves (mg/g^{-1}); N_{root}, nitrogen concentration in root (mg/g^{-1}); NRE, nitrogen resoption efficiency; and NUE, nitrogen use efficiency (g/g^{-1}).

	N_{green}	$N_{senesced}$	N_{root}	NRE	NUE
N_{green}	–	0.53**	0.57*	0.43*	−0.49***
$N_{senesced}$	–	–	0.48ns	−0.51**	−0.94***
N_{root}	–	–	–	−0.04ns	−0.49ns
NRE	–	–	–	–	0.54**
NUE	–	–	–	–	–

Ns, non-significant.
* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.

Because of the high proportion of variance explained by the first PCA axis, individual plant scores were used in all subsequent analyses as a proxy for plantís relative-age. We standardized the values of the PC1 in order to avoid negative values. We used the relative age index as an independent variable to regress nitrogen concentrations in green and senesced leaves, nitrogen concentration in roots, resorption efficiency and NUE.

2.3. Chemical analyses and calculations

Plants were oven-dried for 72 h at 50 °C. Total biomass of individual plants was measured, as well as dry matter of senesced leaves, green leaves and roots. Petioles were included as a component of leaves. Nitrogen concentration was determined by standard Kjeldahl acid digestion method for all individuals. Chemical analyses were carried out for roots and undamaged leaves of type 1 and 2. Root biomass was not always enough to perform chemical analysis. In those cases, two or more plants were pooled to yield the required amount of biomass. We calculated nitrogen resorption efficiency (NRE) on a mass basis (Killingbeck, 1996):

$$\mathrm{NRE} = \frac{(N_{green} - N_{senesced})}{N_{green}},$$

where N_{green} and $N_{senesced}$ are the nitrogen concentrations in green and senesced leaves, respectively. Resorption proficiency was estimated as the concentration of nitrogen in senesced leaves. Low nitrogen concentration implies high proficiency and vice-versa (Killingbeck, 1996). Proficiency can be viewed as a measure of the completeness of nitrogen resorption in terms of proximity to the theoretical lower limit of the nitrogen concentration in senesced leaves (Lü et al., 2012).

Leaf-level nitrogen use efficiency (NUE) was calculated according to Vitousek (1982):

$$\mathrm{NUE} = \frac{1}{(N_{green} - (1 - \mathrm{NRE})}$$

2.4. Statistical analyses

Linear regression analysis was used to assess the effect of the relative-age on nitrogen concentration of roots, green and senesced leaves, NRE and NUE. Comparison of slopes of the regression of N_{green} and $N_{senesced}$ against age was carried out based on one-factor analysis of covariance (ANCOVA). To assess relationships among all variables we perform a Pearson's correlation analysis. We carried out Levene's and Shapiro-Wilk's tests in order to check homogeneity of variances and normality, respectively. Statistical analyses were done using InfoStat 2009.

3. Results

Nitrogen concentration of green leaves (N_{green}) and senesced leaves ($N_{senesced}$) decreased with age ($P<0.01$; $F=15.4$ and $F=19.4$, respectively; Fig. 2A). The slope of decrease of nitrogen concentration was similar in green and senesced leaves ($P>0.05$; $F=3.96$; Fig. 2A).

Nitrogen concentration in roots (N_{roots}) also decreased with age ($P<0.01$, $F=49.7$; Fig. 2 B). The slope of the decrease of nitrogen concentration was similar in roots and green leaves ($P>0.05$; $F=0.9$; Fig. 2A).

Resorption efficiency did not changed with age ($P>0.05$; $F=1.69$; Fig. 3A). Despite this, older plants had higher NUE ($P<0.01$; $F=15.6$; Fig. 3B).

There was a positive relationship between N_{green} and roots N_{root}; this response indicates that the herarchy of N allocation did not change with age (Table 1). The stability of resorption efficiency with age (Fig. 3A) was the result of its positive relationship with N_{green} and its negative relation with $N_{senesced}$ (Table 1). NUE was related negatively with $N_{senesced}$ and N_{green}, and positively with efficiency (Table 1).

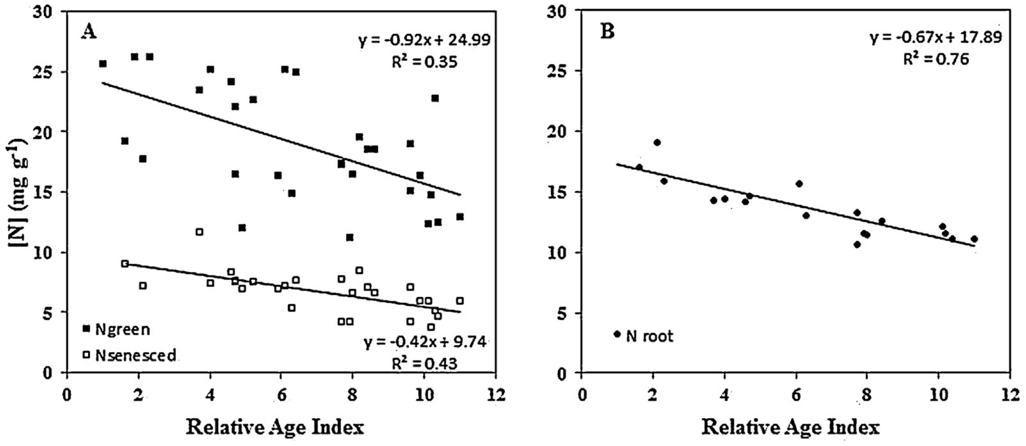

Fig. 2. Effects of age on (A) N concentration in green (filled squares, N_{green}) and senesced leaves (empty squares, $N_{senesced}$), and (B) N concentration in root (filled circles, N_{root}), of *P. mendocina*. Plant relative age index is defined by the scores of an axis of PCA constructed on four morphological traits (see Materials and Methods section). Data were fitted by linear regression.

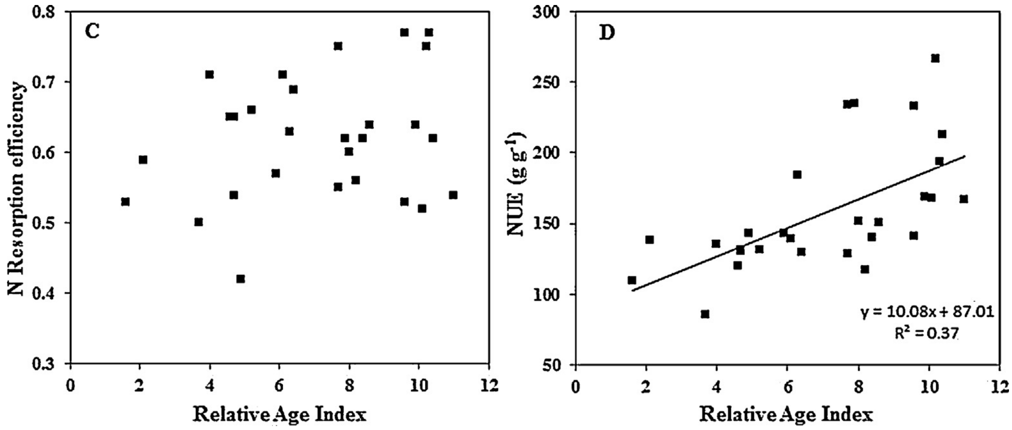

Fig. 3. Relationships between relative age index and, (A) N-resoption efficiency and, (B) Nitrogen use efficiency (NUE) in the perennial *P. mendocina*. Data were fitted by linear regression.

4. Discussion

4.1. Age related changes

Previous studies have shown that in low-input systems plants tend to become more conservative as they grow (Mediavilla et al., 2013). Leaves become thicker (England and Attiwill, 2006), with longer life-spans (Mediavilla et al., 2013) and lower photosynthetic capacity (Niinemets, 2004). These foliar traits have been linked to lower growth rates (Rufty et al., 1988; Chapin, 1991), and this, in turn, is an adaptive response to increasing nitrogen limitation (Nacry et al., 2013). In this context, we raised the question whether nitrogen use and conservation could be affected by the relative age of a plant. Our results indicate the existence of age-related changes in nitrogen concentration in green leaves, roots, resorption proficiency and NUE, with older plants being more efficient in the use of nitrogen than younger ones.

Younger plants showed higher concentrations of nitrogen both in green leaves and roots; this might be explain because plants in early ontogenetic stages are more prone to acquire and utilize resources at a faster rate than adults (Mediavilla et al., 2013). Although we might expect an age-related increase in nitrogen concentration in roots and a concomitant decrease in leaves due to changes in allocation patterns (Niinemets, 2004), in our experiment nitrogen concentration decreased in both organs as plants grew older. These results might indicate a lower acquisition or availability (Aerts, 1996; Lü et al., 2012).

We also found that proficiency increased with age. Killingbeck (1996) suggested that plants with concentrations in senesced leaves lower than $7\,mg\,g^{-1}$ are highly proficient. Following this suggestion, our older plants can be considered very proficient ($5.12\,mg\,g^{-1}$) while the younger ones were less proficient ($9.32\,mg\,g^{-1}$). A possible explanation for this pattern is that younger plants tend to be more acquisitive, a characteristic linked to lower proficiency at the leaf level (Freschet et al., 2010). The higher capacity of acquisition of younger plants might be a consequence of low costs of acquisition compared to the cost of resorption of nitrogen. As plant aged, acquisition capacity decreases (Hodge, 2004) and its cost increases over that of resorption (Gower et al., 1996; Wright and Westoby, 2003; Fisher et al., 2010).

In spite of changes in proficiency, we observed no variation in resorption efficiency, although in other studies a pattern of change with age and size has been found (Yuan et al., 2004; Yuan and Chen, 2010,). Some studies found a negative relation between N_{green} and resorption efficiency, suggesting that plants in low input systems might have higher efficiency (Kobe et al., 2005; Norris and Reich, 2009; Vergutz et al., 2012). However, many other studies (see for example, Aerts, 1996; Killingbeck, 1996; Kazakou et al., 2007; Hättenschwiler et al., 2008; Yuan and Chen, 2009) did not find a clear relationship between resorption efficiency and N_{green}. Our data show that in *P. mendocina* exists a positive relation between these traits, even though it is not strong enough to provoke significant changes in resorption efficiency with age. Given that resorption efficiency is influenced both by N_{green} and $N_{senesced}$ (Killingbeck, 1996; Carrera et al., 2003), constancy in resorption efficiency is explained by the lack of differences in the slopes of N_{green} and $N_{senesced}$. This pattern is confirmed in the correlation analysis were N_{green} and $N_{senesced}$ had an opposite sign and similar weight influence upon resorption efficiency.

NUE was positively related to age. Proficiency is the main factor determining this change (Vitousek, 1982). In this sense, in older plants lower acquisition may lead to low N_{green}, and, in turn, low N_{green} to high proficiency and high NUE.

4.2. Implications for perennial domestication

Our results show that Nitrogen use efficiency (NUE) increases with age. At the plant level, changes in NUE and proficiency should have important implications for plant growth, reproduction and competitive ability (May and Killingbeck, 1992; Aerts, 1999). At the crop level, plant nutrient conservation is expected to generate agronomical and ecological advantages, such as stability in seed yield (Jackson and Koch, 1997), lower reliance on external inputs (Pimentel et al., 2012) and avoidance of fertility loss in soil (Malézieux, 2012). However, it has been shown that domestication using seed-yield as a selection criterion in perennial *Physaria* results in a shift in resource use strategy, from conservative to acquisitive (Vilela and González-Paleo, 2015), which implies less efficient nutrient use (Poorter, 1989). It has been suggested (Dawson et al., 2008) that high NUE throughout the life of a perennial is a desirable trait that should be included in breeding programs in order to meet high productivity and sustainability.

Empirical information on the effect of domestication on nutrient acquisition and use efficiency throughout the life cycle of perennial crops is scarce and little is known on how traits other than those directly targeted, have evolved through breeding. Still, this knowledge is crucial when defining new criteria of selection in crops specifically targeted to arid land (González-Paleo and Ravetta, 2011). We have identified a few questions as directions for future research: Does high-yield selection increase nitrogen loss by senescence? Are age-related changes in proficiency and NUE retained when plants are domesticated using seed-yield as a selection criterion? Is the decrease in domesticated plants longevity a result of changes in the ontogenetic pattern of NUE? Answers to these questions are relevant in an applied context of breeding research.

5. Conclusion

Older plants show higher NUE due to an increase in proficiency with age. This relationship was, in part, modulated by N concentration in green leaves, which, in turn, is controlled by nitrogen availability and acquisition. Since arid lands have limited pools of mineral nitrogen and a greater reliance on internal cycling, traits related to nitrogen use efficiency and conservation are highly relevant for plants growing in this environment. Despite its importance, a clear understanding of the mechanism that allows for a more efficient resource use with age is lacking. Studies on the NUE of wild plants and populations could aid in designing domestication programs and identifying specific traits that are useful for improving performance in low nitrogen environments. In *P. mendocina*, plants with lower rates of nitrogen loss (i.e., more proficient plants) are more efficient and can provide a greater productive potential after a few seasons, compared to plants with a high growth rate and high nitrogen turnover. Since most crop plants were selected in, and for nutrient rich environments, undomesticated wild perennials adapted to low *N* environments such as *P. mendocina*, might be useful sources of genes for increasing NUE in nutrient limited environments.

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