Phenotypic plasticity of Artemisia ordosica seedlings in response to different levels of calcium carbonate in soil postprint

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Date: 2018-11-23T00:00:00+00:00

Abstract

Plant phenotypic plasticity is a common feature that is crucial for explaining interspecific competition, dynamics and biological evolution of plant communities. In this study, we tested the effects of soil CaCO3 (calcium carbonate) on the phenotypic plasticity of a psammophyte, Artemisia ordosica, an important plant species on sandy lands in arid and semi-arid areas of China, by performing pot experiments under different CaCO3 contents with a two-factor randomized block design and two orthogonal designs. We analyzed the growth responses (including plant height, root length, shoot-leaf biomass and root biomass) of A. ordosica seedlings to different soil CaCO3 contents. The results revealed that, with a greater soil CaCO3 content, A. ordosica seedlings gradually grew more slowly, with their relative growth rates of plant height, root length, shoot-leaf biomass and root biomass all decreasing significantly. Root N/P ratios showed significant negative correlations with the relative growth rates of plant height, shoot-leaf biomass and root length of A. ordosica seedlings; however, the relative growth rate of root length increased significantly with the root P concentration increased, showing a positive correlation. These results demonstrate that soil CaCO3 reduces the local P availability in soil, which produces a non-adaptive phenotypic plasticity to A. ordosica seedlings. This study should prove useful for planning and promoting the restoration of damaged/degraded vegetation in arid and semi-arid areas of China.

Full Text

Preamble

Phenotypic plasticity of *Artemisia ordosica* seedlings in response to different levels of calcium carbonate in soil

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Abstract: Plant phenotypic plasticity is a common feature that is crucial for explaining interspecific competition, community dynamics, and biological evolution in plant communities. In this study, we investigated the effects of soil CaCO (calcium carbonate) on the phenotypic plasticity of *Artemisia ordosica*, a psammophyte species that plays an important role on sandy lands in arid and semi-arid regions of China. We conducted pot experiments using a two-factor randomized block design and two orthogonal designs with varying soil CaCO contents, analyzing growth responses including plant height, root length, shoot-leaf biomass, and root biomass. The results revealed that as soil CaCO content increased, *A. ordosica* seedlings exhibited progressively slower growth, with significant decreases in relative growth rates for plant height, root length, shoot-leaf biomass, and root biomass.

Root N/P ratios showed significant negative correlations with the relative growth rates of plant height, shoot-leaf biomass, and root length in *A. ordosica* seedlings. However, the relative growth rate of root length increased significantly with rising root P concentration, demonstrating a positive correlation. These findings indicate that soil CaCO reduces local P availability, thereby inducing non-adaptive phenotypic plasticity in *A. ordosica* seedlings. This study provides valuable insights for planning and promoting restoration of damaged or degraded vegetation in arid and semi-arid areas of China.

Keywords: *Artemisia ordosica*; N/P ratio; phenotypic plasticity; relative growth rate; soil CaCO ; soil P availability; arid and semi-arid areas

Citation: XUE Pingping, ZHAO Xuelai, GAO Yubao, HE Xingdong. 2018. Phenotypic plasticity of *Artemisia ordosica* seedlings in response to different levels of calcium carbonate in soil. *Journal of Arid Land*. https://doi.org/10.1007/s40333-018-0072-4.

1 Introduction

Phenotypic plasticity refers to the phenotypic variation produced by a single genotype in response to different local environmental conditions (Bradshaw, 1965; Lauri et al., 2016; Li et al., 2016). It is inherently a developmental and multivariate phenomenon (Pigliucci et al., 1997). Various environmental factors —including light, temperature, water, heat, and wind—can individually or jointly induce phenotypic plasticity (Sultan, 2001a, b; Pigliucci and Kolodynska, 2002). Importantly, the plasticity of specific functional traits may itself be heritable and thus capable of independent evolution under natural selection (Jain and Bradshaw, 1966; Stearns, 1989; D' Ambrosio and Colagè, 2017). Quantifying phenotypic plasticity in plants can reveal relationships between individual plasticity and ecological and evolutionary patterns (Schlichting, 1986; Bradshaw and Hardwick, 1989; Pigliucci, 2005). Moreover, as sessile organisms, plants rely on phenotypic plasticity to cope with sudden environmental changes (Via et al., 1995; Pigliucci, 2002; Bossdorf and Pigliucci, 2009), which can facilitate species invasions (Geng et al., 2004) and influence patterns of evolutionary diversity (Ghalambor et al., 2007; Fusco and Minelli, 2010; Storz et al., 2010).

Soils at latitudes 10°–40° in both hemispheres generally contain CaCO (Schinas and Rowell, 1977). Abbas et al. (1991) classified plant species as calcicole (thriving in lime-rich soil), calcifuge (not growing well in lime-rich soil), or CaCO -indifferent based on their survival ability in CaCO -rich soils. Nearly 57 years ago, Lee and Woolhouse (1971) investigated bicarbonate effects on root growth in calcicole and calcifuge grasses, finding that calcifuge species were more strongly inhibited by soil CaCO than calcicole species. Interestingly, Pedersen et al. (2011) demonstrated in a pot experiment that both the calcicole species *Anisantha tectorum* and the calcifuge species *Rumex acetosella* grew slower in subsoil containing approximately 10% CaCO than in topsoil with less than 1% CaCO . Our previous study suggested that the ratio of soil CaCO to available P could significantly influence plant density in *Artemisia ordosica* populations (Zhao et al., 2012), indicating that soil CaCO might induce phenotypic plasticity in this species.

This raises an intriguing question: since CaCO itself is a soil-forming substrate, how might it induce plant phenotypic plasticity? We hypothesized that soil CaCO limits P availability, preventing P absorption by plants and thereby affecting N/P ratios, growth rates, and phenotypic plasticity. In this study, we selected *A. ordosica* for three pot experiments analyzing its phenotypic plasticity under varying soil CaCO contents. Our aims were: (1) to examine the effect of soil CaCO content on phenotypic plasticity in *A. ordosica*, and (2) to explore the mechanisms underlying the relationship between soil CaCO content and plant phenotypic plasticity in arid and semi-arid environments.

2.1 Greenhouse pot experiments

Artemisia ordosica is a dominant psammophyte species that forms communities on sandy lands in arid and semi-arid areas of Northwest China. Restoration of *A. ordosica*-dominated plant communities is currently crucial for controlling degraded vegetation ecosystems in the study region (Wang et al., 2018).

The pot experiments were conducted in March 2012 at the greenhouse of the Department of Plant Biology and Ecology, Nankai University, China. Seeds of *A. ordosica* and experimental soil were collected from Bayanhot in Alxa Left Banner, Inner Mongolia Autonomous Region, China.

To investigate *A. ordosica* growth in soils with varying CaCO contents, we performed three pot experiments using a two-factor randomized block design and two orthogonal designs. In the low soil CaCO content orthogonal experiment with an L8 (4×24) array, soil CaCO levels were 0 (control), 10, 25, and 50 g/kg. In the high soil CaCO content orthogonal experiment with an L16 (45) array, soil CaCO levels were 0 (control), 25, 50, and 100 g/kg, soil available P levels were 0, 3, 6, and 12 g/kg, and watering amounts were 200, 250, 300, and

350 mL/week. In the two-factor randomized block experiment with high soil CaCO content, soil CaCO levels were 10, 50, 75, and 100 g/kg, and watering levels were 250, 300, 350, and 400 mL/week, respectively. All three experiments included three replicates per treatment.

The seed sowing procedure was as follows: seeds were sown at 3-4 seeds per hole in seedling-raising pans filled with a 1:1 turf:perlite mixture. The pans were covered with a thin moist paper film to reduce evaporation until germination occurred. After 25 days, germinated seedlings were transferred to polyvinyl chloride (PVC) pots (170 mm × 200 mm; one seedling per pot) according to the experimental design. Each pot contained 2 kg of mixed soil at a 2:1 sandy soil:loam ratio, with the mixture containing 3.11 g/kg organic matter, 7.00 mg/kg available N, and 5.77 mg/kg available P.

To calculate relative growth rate (RGR) of potted seedlings, we measured all initial plant heights upon transfer to PVC pots. Additionally, 50 leftover *A. ordosica* seedlings from the seedling-raising pans served as initial controls. These seedlings were excavated, washed to remove root mud, blotted with filter paper, and measured for plant height, root length, and fresh weights of shoot-leaf and root biomass.

The *A. ordosica* seedlings were then grown for a 40-day monitoring period. To minimize water evaporation, we watered all seedlings by injecting water beneath the soil surface to a depth of 2 cm using a syringe. Greenhouse temperatures were maintained at 25°C during daytime and 18°C at night. Upon harvest, we measured and recorded plant height, root length, shoot-leaf biomass, and root biomass for every seedling.

2.2 Sample analyses

For seedlings in the high soil CaCO content experiment, plant N and P concentrations were determined using H SO -H O -semi-micro-Kjeldahl and H SO -H O -Mo-Sb-Vc-colormetry methods, respectively (Bao, 2007). Each plant root sample was analyzed with three measurement replicates.

2.3 Calculation of RGR

We used 50 leftover *A. ordosica* seedlings for curve regressions with plant height as the independent variable and shoot-leaf biomass, root length, and root biomass as separate dependent variables. Because all regression equations were significant ($P < 0.001$), they were used to estimate pre-experiment shoot-leaf biomass, root length, and root biomass of the potted seedlings.

The RGR values for plant height, root length, shoot-leaf biomass, and root biomass of *A. ordosica* seedlings were calculated as follows:

$$\mu = \frac{\ln(M_t/M_0)}{t} \quad (1)$$

where is the relative growth rate of plant height (cm/cm/d), root length (cm/cm/d), shoot-leaf biomass (g/g/d), or root biomass (g/g/d); M is the observed pre-experiment plant height (cm) or shoot biomass (g), root length (cm), or root biomass (g) predicted from the regression equations; M is the post-experiment measurement of the four growth response variables; and t is the growing time (40 d).

2.4 Data analysis

Data were analyzed using SPSS 13.0 software (SPSS, Chicago, Illinois, USA) with two-way ANOVA. Homogeneity tests were performed first, followed by Duncan' s test for comparing means between groups with equal variances. Tamhane' s T2 test was used for groups with unequal variances.

3.1 Effects of low soil CaCO content on *A. ordosica* seedling growth

In the low soil CaCO content orthogonal experiment, *A. ordosica* seedlings treated with 50 g/kg soil CaCO showed reductions of 69.29%, 46.18%, 87.88%, and 66.75% in plant height, root length, shoot-leaf biomass, and root biomass, respectively, compared to the control. As shown in Figure 1 [Figure 1: see original paper], the RGR values for all four growth response variables were lowest under the highest soil CaCO content and highest under the lowest content.

3.2 Effects of high soil CaCO content on *A. ordosica* seedling growth

In the high soil CaCO content two-factor randomized block experiment, RGR values for plant height and shoot-leaf biomass decreased significantly with increasing soil CaCO content, while RGR values for root length and root biomass also declined but not significantly (Fig. 2a [Figure 2: see original paper]). In this experiment, watering level treatments showed no significant effects on any growth response variable ($P > 0.05$) (data not shown).

In the high soil CaCO content orthogonal experiment, soil available P and watering amount treatments had no significant effects on any growth response variable ($P > 0.05$) (data not shown). Soil CaCO content did not significantly influence RGR values for plant height, shoot-leaf biomass, or root biomass, but it did significantly and negatively impact root length RGR (Fig. 2b).

3.3 Relationships of RGR with root N/P ratio and root P concentration in *A. ordosica* seedlings

Regression analyses revealed that under high soil CaCO content, *A. ordosica* seedlings with higher root N/P ratios exhibited lower RGR values for plant height (Fig. 3a [Figure 3: see original paper]) and shoot-leaf biomass (Fig. 3b) in the two-factor randomized block experiment, and lower root length RGR in the orthogonal experiment (Fig. 3c). A significant positive logarithmic relationship was observed between root length RGR and root P concentration in the orthogonal experiment (Fig. 3d). In other words, root length RGR in *A. ordosica* seedlings decreased significantly with increasing root N/P ratio but increased significantly with rising root P concentration.

4 Discussion

Soil CaCO can exert complex influences on plant phenotypic plasticity. In this study, CaCO additions significantly affected RGR values for plant height, shoot-leaf biomass, and root length in *A. ordosica* seedlings, as did soil available P concentrations under high CaCO conditions. Higher soil CaCO contents reduced growth in plant height, root length, shoot-leaf biomass, and root biomass of *A. ordosica* seedlings, demonstrating that soil CaCO can affect phenotypic plasticity. This is an intriguing phenomenon, as CaCO molecules are neutral. How might they influence seedling growth rates? One plausible explanation is that CaCO made the soil "tighter," increasing water retention and hindering seedling water uptake, thereby adversely affecting growth. Another mechanistic explanation is that added CaCO strongly reduced soil P availability, further limiting growth of water-stressed *A. ordosica* seedlings. Regardless of the mechanism, soil CaCO additions reduced the growth potential of *A. ordosica* seedlings.

Notably, root length growth in *A. ordosica* seedlings gradually declined under higher soil CaCO contents. Root length was constrained rather than promoted by high soil CaCO , likely because the anterior root extremities decayed during early seedling growth. When *A. ordosica* seedlings were transferred from seedling-raising pans (filled with 1:1 turf:perlite) to PVC pots (filled with sandy loam containing CaCO), some decayed roots probably died, with higher soil CaCO content causing more root death. Thus, CaCO additions prevented root length expansion in *A. ordosica* seedlings.

Kerley (2000) observed growth plasticity in *Lupinus albus* when exposed to limed soil profiles. In our study, increased soil CaCO contents progressively decreased plant height, root length, shoot-leaf biomass, and root biomass in *A. ordosica* seedlings. During the 40-day growth period, seedlings treated with 50 g/kg soil CaCO showed reductions of 69.29%, 46.18%, 87.88%, and 66.75% in plant height, root length, shoot-leaf biomass, and root biomass, respectively, compared to controls, with corresponding RGR reductions of 89.99%, 145.41%, 111.73%, and 78.90%. Clearly, soil CaCO can inhibit growth plasticity in *A. ordosica* seedlings. While soil CaCO is a soil formation matrix, its influence on plant growth differs from other ecological factors such as light, temperature, water, heat, wind, soil nutrients, and salinity (Fan et al., 2012; Zheng et al., 2012). Our results suggest that soil CaCO represents an abiotic stress factor for *A. ordosica* in arid and semi-arid Northwest China. As Ghalambor et al. (2007) noted, adaptive phenotypic plasticity favors plant establishment in new habitats, while non-adaptive plasticity corresponds with stressful environments. In this context, soil CaCO appears to generate non-adaptive phenotypic plasticity.

The inhibition of growth plasticity in *A. ordosica* seedlings by soil CaCO was essentially due to restricted P absorption. In calcareous soils of arid and semi-arid regions, approximately 70% of total inorganic P exists as Ca-P complexes (Ma et al., 2009). Among soil inorganic P pools, only Ca -P was used here to simplify the more complex 0.5 M NaHCO (pH 7.5)-soluble P form, which significantly affects soil available P levels (Ma et al., 2009). Soil CaCO accumulation maintains soil pH at 7.0–8.0, reducing P availability and restricting plant P utilization rates (Reinbott and Blevins, 1999; Li et al., 2004; Wojewodzic et al., 2011). P restriction inhibits plant growth primarily by altering plant C/N/P stoichiometry (Ehlers et al., 2010; Persson et al., 2011; Cai et al., 2012). In arid and semi-arid regions where P is crucial for plant growth (Pajaei et al., 2018), altered P concentrations can change plant N/P ratios (He et al., 2016; Martinez-Oro et al., 2017). The growth rate hypothesis proposed by Elser et al. (2010) states that plant specific growth rate is negatively related to N/P ratio (Matzek and Vitousek, 2009). Our results showing decreased RGR values for growth response variables (plant height, root-leaf biomass, and root length) with higher N/P ratios in *A. ordosica* seedlings are consistent with this hypothesis.

Plant roots are particularly sensitive to environmental change (Qiu et al., 2017). In this study, root length in *A. ordosica* seedlings showed a negative response to higher soil CaCO contents. Our follow-up analysis suggested that root length growth increased with higher root P concentrations, implying that the influence of root N/P ratio on root length RGR occurred via CaCO effects on P absorption. Thus, higher soil CaCO contents resulted in lower P concentrations in *A. ordosica* seedlings, consequently affecting their phenotypic plasticity.

5 Conclusions

Soil CaCO is clearly a stress factor that adversely affects *A. ordosica* seedling growth. Regardless of whether CaCO contents are lower (<50 g/kg) or higher (>50 g/kg), soil CaCO additions slow *A. ordosica* seedling growth. Therefore, soil CaCO induces non-adaptive phenotypic plasticity in *A. ordosica* seedlings. Under high soil CaCO contents, RGR values for plant height, shoot-leaf biomass, and root length all decreased significantly with increasing root N/P ratio, while root length RGR increased significantly with rising root P concentration. Thus, altered root P concentration is the primary driver of phenotypic plasticity in *A. ordosica* seedlings.

Acknowledgments

This research was supported by the National Key Research and Development Program of China (2016YFC0500706).

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