



IS PLASTICITY IN RESPONSE TO LIGHT AND TO SOIL INVOLVED IN THE ECOTYPIC DIFFERENTIATION OF A TREE SPECIES FROM CERRADO AND ATLANTIC FOREST?

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INTRODUCTION

Phenotypic plasticity is the ability of a given genotype of rendering different phenotypes under different environmental conditions. Plasticity can be in itself a trait subject to natural selection and differences in plasticity among genotypes can be the result of specialization to a fraction of the environmental heterogeneity (Ghalambor *et al.*, 2007). The responses of species and population to different environmental conditions are known as *sensu lato* phenotypic plasticity (Valladares *et al.*, 2006), which is not strictly the evaluation of a single genotype under different environments. This is an important approach in determining the implications of plasticity for the distribution, spread and persistence of populations, and also for understanding patterns of evolutionary diversification (Sultan 2000).

The Brazilian Cerrado and Atlantic Forest are adjacent biomes with different main environmental conditions. While the first is a tropical forest with dense canopy and comparatively more mesic environmental conditions, the Cerrado biome ranges from grassland to woodland, being the most frequently physiognomic type a xeromorphic savanna generally found in poor, well - drained and acid soils. Tree species from Atlantic Forest and Cerrado typically conform very distinct functional types, differing in physiological, morphological and life history attributes (Hoffmann *et al.*, 2005). Few tree species show distribution across both biomes, among them there is *Plathymenia reticulata* (Leguminosae-Mimosoideae).

OBJECTIVES

The existence of local adaptation in populations of this tree species is here investigated, hypothesizing that phenotypic plasticity in response to light and to soil are involved in eco-

typic differentiation between Atlantic Forest and Cerrado populations.

MATERIAL AND METHODS

We evaluated four populations of *P. reticulata* from which seeds were collected as mixed samples from 10 individuals. Two populations are characterized as the Atlantic Forest semi - deciduous physiognomy, one located in the biome core area (19°45'S 43°31'W) and the other one in its periphery, in an ecotone with the Cerrado (19°56'S 46°56'W). The two other evaluated populations are in the Cerrado biome, one located in the core area of the biome (18°43'S 45°03'W) and the other one in its periphery, in an ecotone with the Atlantic Forest (19°49'S 43°48'W).

Seedlings were planted in pots and cultivated in a common garden experiment, they were submitted to two different experiments. In the light experiment, twenty individuals from each population were grown in shade (22% of full sunlight) and twenty in full sunlight condition. In the soil experiment, twenty individuals from each population were grown in soil from Cerrado and twenty in soil from Atlantic Forest. Chemical analysis of soil types showed that they differ mainly in organic matter (18 and 28.4 g/kg for Cerrado and Atlantic Forest soil respectively), C (1.0 and 1.4 g/kg), N (1.0 and 1.4 g/kg), base saturation (17.01 and 44.01%) and aluminum saturation (58.39 and 9.21%).

After six months of growth, the following morphological data were taken: shoot length (cm), mean internode length (cm) [shoot length (cm)/ number of internodes], slenderness index [shoot length (cm) / base diameter (mm)]. In vivo chlorophyll fluorescence measures were made with the use of a pulse amplitude modulated photosynthesis yield analyser. Potential quantum yield of photosystem II was calculated (Fv/Fm), light saturation curves were obtained

in order to determinate the maximum apparent photosynthetic electron transport rate (ETR_{max}) and saturating photosynthetically active photon flux density ($PPFD_{sat}$), following Rascher *et al.*, (2000). Leaf pigments content expressed in fresh weight basis (total chlorophylls, carotenoids:chlorophyll ratio and chlorophyll a:b ratio) were estimated following Lichtenthaler and Wellburn (1983).

For each population, plasticity in response to light and in response to soil were estimated using the Relative Distance Phenotypic Index (RDPI) described by Valladares *et al.*, (2006). For each trait, comparison of RDPIs among populations were made by ANOVAs and post hoc Tukey test, or by Kruskal - Wallis and post hoc Holm test when non parametrical distributions were found. For each trait, comparisons among light and soil RDPIs' were made by T - test.

RESULTS AND DISCUSSION

Plasticity in response to light

Phenotypic plasticity in response to light was comparatively higher for chlorophyll (RDPI=0.36) and lower for Fv/Fm (RDPI=0.03), with intermediate values for the other traits (RDPI between 0.12 and 0.19). Comparisons of plasticity in response to light among populations showed that for shoot length and slenderness index, plasticity was higher in Atlantic Forest core population (respectively Ch - $sq=86.69$, $p < 0.001$ and Ch - $sq=56.626.69$, $p < 0.001$), while for leaf pigments contents higher plasticity was found either in Atlantic Forest core or both ecotonal populations (total chlorophyll: $F=10.49$, $p < 0.001$; carotenoids:chlorophyll ratio: Ch - $sq=15.70$, $p < 0.01$; chlorophyll a:b ratio: Ch - $sq=9.67$, $p < 0.05$). Traits such as internode length and the ones related to photosynthetic response did not show differences in plasticity among populations ($p > 0.05$).

Lower plasticity values were recurrently found in Cerrado core population, considering traits' indexes that significantly differed among populations. This result indicates that comparatively higher plasticity in response to light is found in Atlantic Forest populations than Cerrado. This pattern can be interpreted as habitat based selection for plasticity. Higher morphological plasticity in response to light in Atlantic Forest individuals suggests higher efficiency in exploiting this limiting resource than plants from Cerrado. Morphological plasticity has been linked to an enhanced capacity to survive and grow in the understory (Valladares *et al.*, 2000b) as a particular mechanism to optimize resource acquisition in plants (West - Eberhard 1989). The evolutionary advantage and the benefits of plasticity are better understood than its disadvantages, limits and costs (DeWitt *et al.*, 1998), but a reduced plasticity can be advantageous under stressful conditions where a conservative resource use is crucial (Valladares *et al.*, 2007). In this context, lower plasticity in response to light in Cerrado may a feature related to the stress resistance syndrome (Chapin *et al.*, 1993). The lower plasticity could prevent Cerrado plants under a temporally favorable circumstance to grow too large or to produce structures that are too expensive to be sustained once conditions deteriorate, as has been

discussed for evergreen woody plants in both tropical and Mediterranean ecosystems (Valladares *et al.*, 2000a, b).

Plasticity in response to soil

Phenotypic plasticity in response to soil was comparatively higher for shoot length (RDPI=0.22) and lower for Fv/Fm and carotenoids:chlorophyll ratio (RDPI < 0.10), with intermediate values for the other traits (RDPI between 0.12 and 0.17). Comparisons of plasticity among populations showed that for shoot length higher plasticity was found in Atlantic Forest core population (Ch - $sq=17.18$, $p < 0.01$). The traits slenderness index, internode length, Fv/Fm and chlorophyll a:b ratio, showed a major tendency of higher plasticity in ecotonal populations while compared to core ones (respectively Ch - $sq=17.32$, $p < 0.01$; Ch - $sq=9.81$, $p < 0.05$; Ch - $sq=8.52.70$, $p < 0.05$ and Ch - $sq=9.65.70$, $p < 0.05$). For $PPFD_{sat}$ significantly higher plasticity was found in Atlantic Forest in ecotone, followed by the core populations and lower values in Cerrado in ecotone (Ch - $sq=12.34$, $p < 0.01$). No significant differences in plasticity among populations were found for ETR_{max} , chlorophyll content and carotenoids:chlorophyll ratio ($p > 0.05$).

The evaluated traits showed a general pattern of higher plasticity in response to soil in populations from ecotonal area when compared to Atlantic Forest and Cerrado core. Higher plasticity in ecotonal populations could be explained as a strategy of plants located in the boundary between biomes to adjust to different soil environments, considering that plasticity is important in the process of colonizing new ecological space (West - Eberhard 1989).

Comparisons between plasticity in response to light and soil

While comparing plastic responses to soil and to light, we found that for chlorophyll and carotenoids:chlorophyll ratio plasticity in response to light is significantly higher than in response to soil (respectively $t=4.120$, $p < 0.001$ and $t=2.460$, $p < 0.05$). This result is in accordance to the fact that leaf pigments content are more strongly influenced by light than soil. All the other evaluated traits showed to be equally plastic in response to light and soil ($p > 0.05$), showing that, for most of the traits, populations of *P. reticulata* are equally plastic in response to these two different environmental factors.

CONCLUSION

In a general way, *P. reticulata* populations from Cerrado, Atlantic Forest and ecotonal areas between biomes are equally plasticity in response to light and soil for most of the evaluated morphological and physiological traits. However, responses to light and soil drive processes in different directions: responses to light show a major pattern of higher plasticity in Atlantic Forest than in Cerrado populations, showing ecotypic differentiation between populations from different biomes; this ecotypic difference was not corroborated by responses to soil, for which higher plasticity was found in ecotonal populations.

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