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Linking mycorrhizal fungi and soil nutrients to vegetative and reproductive ruderal plant development in a fragmented forest at central Argentina

G. Grilli *, C. Urcelay, L. Galetto

Instituto Multidisciplinario de Biología Vegetal (CONICET-UNC), Vélez Sarsfield 1611, CC 495, 5000 Córdoba, Argentina
FCEFyN, Universidad Nacional de Córdoba, Córdoba, Argentina

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ABSTRACT

We studied the actual links between mycorrhizal fungi, nutrient availability and plant development in several sites of fragmented Chaco forests. Specifically, we evaluated whether arbuscular mycorrhizal fungi (AMF) and dark septate endophytes (DSE) colonization and availability of soil nutrients are related to growth (biomass and plant height) and reproductive traits (pollen size and pollen and fruit production) of two ruderal, annual, congeneric *Euphorbia* species along a gradient of forest fragmentation. We assessed relationships between forest fragment size and isolation, nutrient availability, mycorrhizal fungal variables and plant development at eleven Chaquean forest fragments (0.5–1000 ha) immersed in an agricultural landscape in central Argentina. Mycorrhizal colonization was not related to forest fragment isolation, positively related to forest fragment size and negatively related to soil nutrient availability in both hosts along the fragmentation gradient. Plant reproductive and vegetative traits were related to mycorrhizal colonization. In general, plant height, biomass, and fruit production were negatively related to AMF, and pollen production was positively related to DSE, in both ruderal hosts (native and exotic). We found remarkable relationships along a forest fragmentation gradient that reliably link forest fragment size to lower nutrient availability and increased mycorrhizal colonization in native/exotic ruderal hosts, while negatively linking AMF colonization to plant development and reproductive success.

1. Introduction

Forests have been increasingly fragmented around the globe in the last decades, principally due to the advances of agricultural and urban frontier (Didham, 2010). Fragmented landscapes have been largely related to ecological patterns and processes of organisms occurring in the aboveground compartment of the ecosystem (Fahrig, 2003; Lindenmayer and Fischer, 2006; Didham et al., 2012). Thus, few studies have focused on relationships between belowground organisms (i.e. mycorrhizal fungi) and the forest fragmentation process (Mangan et al., 2004; Peay et al., 2007; Grilli et al., 2012). In particular, arbuscular mycorrhizal fungi (AMF) and dark septate endophytes (DSE) are the most common and widespread fungal root symbionts. AMF colonize roots of approximately 80% of vascular plant species, and DSE were recorded in more than 600 plant species (Smith and Read, 2008; Newsham, 2011). There is substantial evidence showing that plant identity, nutrient availability and other environmental factors affect AMF colonization (Smith and Read, 2008). Forest fragmentation may be related to the factors affecting AMF colonization, such as exotic plant establishment and soil nutrient content (Lindenmayer and Fischer, 2007; Billings and Gaydess, 2008). We found a negative relationship of nutrient availability to AMF root colonization, spore abundance and diversity in the rhizosphere of two congeneric *Euphorbia* with increasing forest fragment size (Grilli et al., 2012). These complex relationships between forest fragmentation, nutrient availability, and AMF in the plant rhizosphere might be linked to aboveground plant growth and reproduction. However, most studies involving functional effects of forest fragmentation on plants have focused on aboveground biotic interactions, such as pollination and/or fruit dispersal, particularly in Chaco forests (Aguilar et al., 2006; Galetto et al., 2007; Grilli and Galetto, 2009; Ponce et al., 2012).

It is well known that nutrient acquisition, either directly or mediated by mycorrhizal fungi, varies among plants according to their resource acquisition strategies (Aerts and Chapin, 2000). For instance, functional measurements are difficult in long-lived perennial plant species with slow growth rates, in particular reproductive ones. Therefore, short-life cycle annual plants are a good study case for the understanding of forest dynamics in fragmented landscapes (Tscharntke et al., 2012). Success of ruderal plants in

* Corresponding author. Tel.: +54 3517594502.
E-mail address: ggrilli@imbiv.unc.edu.ar (G. Grilli).

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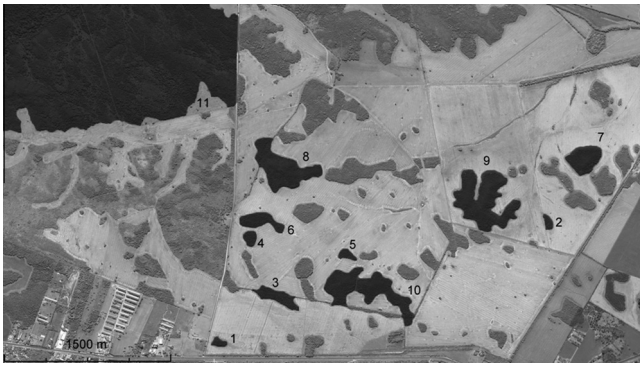

Fig. 1. Study area with the eleven forest fragments studied in black.

Table 1
GLMM outputs of mycorrhizal colonization in two ruderal *Euphorbia* plant species (native and exotic) along a fragmentation gradient ($n = 11$ forest fragments) in Córdoba, Argentina.

Term	d.f.	Deviance (χ^2)	*P*
(a) Total mycorrhizal colonization			
Species	1	41.31	**<0.0001**
LogArea	1	8.97	**0.002**
Isolation	1	1.04	0.31
LogArea * Species * Isolation	4	7.65	0.1
(b) Vesicular colonization			
Species	1	117.43	**<0.0001**
LogArea	1	1.17	0.19
Isolation	1	0.55	0.45
LogArea * Species * Isolation	4	49.25	**<0.0001**
(c) Native vesicular colonization			
LogArea	1	0.01	0.9
Isolation	1	1.18	0.27
(d) Exotic vesicular colonization			
LogArea	1	2.13	0.14
Isolation	1	0.32	0.56
(e) DSE colonization			
Species	1	7.22	**0.007**
LogArea	1	348.16	**<0.0001**
Isolation	1	0.44	0.5
LogArea * Species * Isolation	4	0.47	0.82

Bold values are significant at $P < 0.05$.

disturbed habitats has been attributed to rapid growth rates and to a comparably higher efficiency than other plants in acquiring available nutrients (Grime, 2001). Mycorrhizal fungi have been widely shown to be beneficial to their hosts, mainly due to enhancement in nutrient uptake (Smith and Read, 2008). Conversely, some ruderal plants appear to be less dependent or negatively affected by fungal symbionts (Brundrett, 1991; Hoeksema et al., 2010). In fact, vegetative development in ruderal plants could be negatively affected by AMF (Pérez and Urcelay, 2009; Rinaudo et al., 2010; Veiga et al., 2011; Urcelay et al., 2011). Accordingly, since reproductive traits also depend on resource availability, it might be expected that ruderal plant reproductive traits are also negatively affected by root symbionts (Koide, 2010). Flower, pollen, fruit and seed production might be increased, decreased or not affected by mycorrhizal fungi (Poulton et al., 2001; Poulton et al., 2002; Varga and Kytöviita, 2010; Varga, 2010 and references there in). However, this evidence does not support generalities about relationships between mycorrhizal fungi and hosts with different nutrient acquisition strategy. In this study we worked with two annual ruderal *Euphorbia plants* (exotic and native) that might be affected by forest fragmentation to evaluate the plant development process and its relationship with mycorrhizal fungal traits and nutrient availability. In addition, several studies have shown that the outcome of mycorrhizal associations might differ between native and invasive plant species (reviewed by Pringle et al., 2009). However, how mycorrhizal fungi affect ruderal plants according to their identity in fragmented forests remains unclear.

Table 2
GLMM outputs of mycorrhizal colonization and nutrient availability along a fragmentation gradient ($n = 11$ forest fragments) in Córdoba, Argentina.

Term	d.f.	Deviance (χ^2)	*P*
(a) Total mycorrhizal colonization			
Nitrate	1	4.1	**0.04**
Ammonia	1	0.12	0.73
Phosphorus	1	10.53	**0.001**
Total nitrogen	1	1.28	0.25
Organic matter	1	0.35	0.55
C:N	1	4.77	**0.02**
Organic carbon	1	0.44	0.51
(b) Vesicular colonization			
Nitrate	1	6.48	**0.01**
Ammonia	1	0.8	0.37
Phosphorus	1	6.24	**0.01**
Total nitrogen	1	14.54	**0.0001**
Organic matter	1	2.48	0.12
C:N	1	0.2	0.65
Organic carbon	1	1.83	0.18
(c) DSE colonization			
Nitrate	1	10.43	**0.001**
Ammonia	1	1.62	0.2
Phosphorus	1	10.82	**0.001**
Total nitrogen	1	0.17	0.68
Organic matter	1	0.42	0.52
C:N	1	11.29	**0.0007**
Organic carbon	1	0.46	0.5

Bold values are significant at $P < 0.05$.

The aim of this study was to examine whether plant growth and reproductive traits of two ruderal, annual *Euphorbia* species (*E. acerensis* and *E. dentata*, native and exotic respectively) are related to mycorrhizal colonization and nutrient availability in a forest fragmentation gradient. We predicted that vegetative and reproductive ruderal plant development would be positively related to nutrient availability and negatively related to fungal variables along this forest fragmentation gradient. In this way we expected to provide novel evidence on the links of plant development and reproduction in a forest fragmentation gradient with patterns of mycorrhizal fungi and nutrient availability in a fragmented forest.

2. Methods

2.1. Study site

Chaco forests in central Argentina present high rates of landscape fragmentation (Zak et al., 2004), due to vast landscape modification with most original vegetation having disappeared (Fisher and Lindenmayer, 2007) and thus can be characterized as relictual forests. The study area ranges between 31°11'19"S; 64°16'02"W and 31°13'05"S; 64°15'55"W. The altitude varies from 600 to 640 m above sea level. The rainy season occurs between October and May with a mean annual precipitation of 750 mm (Luti et al., 1979; Moglia and Giménez 1998). Mean maximum and minimum temperatures are 26 and 10 °C, respectively. The vegetation of the semiarid shrub-forest in fragments is characterized by *Aspidosperma quebracho-blanco* Schltdl., *Acacia* spp., *Zanthoxylum coco* Engl., *Prosopis* spp., *Celtis ehrenbergiana* Liebm., native and exotic herbs and grasses, vines and epiphytic plants.