The effects of fire severity on ectomycorrhizal colonization and morphometric features in Pinus pinaster Ait. seedlings

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Abstract

Aim of the study: Mycorrhizal fungi in Mediterranean forests play a key role in the complex process of recovery after wildfires. A broader understanding of an important pyrophytic species as Pinus pinaster and its fungal symbionts is thus necessary for forest restoration purposes. This study aims to assess the effects of ectomycorrhizal symbiosis on maritime pine seedlings and how fire severity affects fungal colonization ability.

Area of study: Central Spain, in a Mediterranean region typically affected by wildfires dominated by Pinus pinaster, a species adapted to fire disturbance.

Material and Methods: We studied P. pinaster root apexes from seedlings grown in soils collected one year after fire in undisturbed sites, sites moderately affected by fire and sites highly affected by fire. Natural ectomycorrhization was observed at the whole root system level as well as at two root vertical sections (0-10 cm and 10-20 cm). We also measured several morphometric traits (tap root length, shoot length, dry biomass of shoots and root/shoot ratio), which were used to test the influence of fire severity and soil chemistry upon them.

Main results: Ectomycorrhizal colonization in undisturbed soils for total and separated root vertical sections was higher than in soils that had been affected by fire to some degree. Inversely, seedling vegetative size increased according to fire severity.

Research highlights: Fire severity affected soil properties and mycorrhizal colonization one year after occurrence, thus affecting plant development. These findings can contribute to a better knowledge of the factors mediating successful establishment of P. pinaster in Mediterranean forests after wildfires.

Keywords: Wildfire; mycorrhizal fungi; Maritime pine; bioassay.

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Introduction

Wildfires constitute the main source of disturbance in Mediterranean forest ecosystems (Gassibe et al., 2011), strongly affecting soil fungi and plant communities (Dahlgberg et al., 2001, Carney & Bastias, 2007, Rincón & Pueyo, 2010). This comes both as a direct result of the high temperatures reached during a forest fire, but also indirectly through changes to soil chemical and physical properties, like a pH increase, enhanced hydrophobicity or changes of available nutrients (Certini, 2005).

Ectomycorrhizal fungi (ECM) play an important role in the colonization of new areas of land or in the restoration of the vegetative community following a disturbance (Claridge et al., 2009, Rincón & Pueyo, 2010). Indeed, survival of tree seedlings strongly depends on the rapid formation of an efficient root system, determined by the development of mycorrhizal symbiosis but also by favourable ecological conditions (Jackson et al., 2007, Palfner et al., 2008). ECM help their plant symbionts by improving water and nutrient uptake from the soil, carbohydrate distribution and production of plant growth regulators and avoiding water losses and root desiccation (Rincón et al., 2007). All this contributes to prevent environmental stress caused by drought (Scattolin...
related traits across
*P. pinaster*
ing fire regimes have even selected for different fire-
forests typically suffer from frequent forest fires. Vary-
puts to new communities, mainly competition-free
munities, at the same time fire also provides large in-
interrelationships between changes in soil properties,
host plant development and associated belowground
al communities associated with *P. pinaster*, showing that
some fungal groups are potentially fire-adapted (Rincón
2014). These findings highlight the interest to
deepen our knowledge on the colonization of *P. pinaster*
seedlings by ECM fungi after wildfires. In this frame-
work, it is particularly interesting to learn about the
interrelationships between changes in soil properties,
and likely different potential for ECM colonization.
A devastating crown-fire occurred in Central Spain
in 2008 providing the opportunity to increase further
this knowledge. Here, we looked at how vegetative
traits of *P. pinaster* seedlings differ when they are
grown in soils exposed to increasing fire severity, hav-
ning as a consequence different biochemical properties
and likely different potential for ECM colonization.
We performed a bioassay experiment under greenhouse
controlled conditions where we analyzed i) seedling
vegetative traits and ii) ECM colonization at two dif-
ferent root vertical sections. We hypothesised that
ECM-colonization would be highest in undisturbed
soils and at upper root sections, and lowest in highly
disturbed soils. We also expected colonization rate to
be correlated with seedling performance.

**Materials and methods**

**Study site**

Our study was performed in Central Spain, in the
Autonomous Community of Castilla y León, the third
European region in size and one of the most strongly
damaged by wildfires. According to the European Forest
Fire Information System (EFFIS), 1996 fires occurred
in the region during 2008 affecting 152.64 km² (Quin-
tano *et al.*, 2011). The fire season occurs during the
period of June-September, corresponding to the warm
to hot and dry summer, typical of Mediterranean climate.
Fire effects on mycorrhization and plant parameters

The study was carried out in Honrubia de la Cuesta (northern part of Segovia province), which is a Mediterranean ecosystem dominated by *Pinus pinaster* plantations established by the Spanish Forest Services in previously deforested areas (440901-443169 longitude-UTM, 4592 704-4590583 latitude-UTM, 750-880 m.a.s.l.). Here, a large wildfire burned 1200 ha of forest and canopies in August 2008 at which pine trees were about 40 years old. This site has a supra-Mediterranean climate with 3 months of dry season in the summer, a mean annual rainfall of 480-500 mm and mean temperatures ranging from 8 to 13 °C. The warmest month is July and the coldest January. These data were provided by the closest meteorological station (Linares del Arroyo 41° 31’ 40´´N, 3º 32´ 72´´W) located 15 km from the study area.

This area is composed of Paleozoic metamorphic rocks, dominated by Ordovician and Silurian shales (Barrenechea & Rodas, 1992). The soil is classified as Inceptisol suborder Xerept (Alvarez et al., 1993).

In the forest understory, sparse individuals of *Cytisus scoparius* (L.) Link, *Quercus faginea* Lam and *Quercus ilex* (L.) ssp. *ballota* (Desf.) Samp. were found. A number of species have been identified during mushroom forays in the area (pers. obs.). Ectomycorrhizal *Colybia* sp., *Cortinarius cinnamomeus* (L.) Fr., *Cylostoma amianthinum* (Scop.) Fayod, *Hebeloma mesophaeum* (Pers.) Quél., *Inocybe* sp., *Laccaria laccata* (Scop.) Cooke, *Rhizopogon luteolus* Fr., *Tricholoma sculpturatum* (Fr.) Quél., and saprophytic *Astraeus hygrometricus*, *Baeospora myosura* (Fr.) Singer, *Colybia butyracea* (Bull.) P. Kumm., *Hemimycena* sp., *Hygrophorus gliocyclus* Fr., *Mycena pura* (Pers.) P. Kumm., *Mycena pura* ssp. *lutea* (Gillet) Arnolds, were observed at sites not affected by fire. While *Galerina* sp., *Gerronema* sp., *Omphalina* sp., *Pholiota carbonaria* (Fr.) Sing., were found in places moderately affected by fire and only pyrophitic *Pholiota carbonaria* was found at those sites fully impacted by the fire. No ECM species were found to form sporocarps in areas affected by fire.

Experimental design and field sampling

Three different sites were chosen within our study area according to the degree of damage caused by fire on vegetation and soil (Figure 1). Fire severity and soil damage were classified following Rincón & Pueyo (2010) and Vega et al. 2013 criteria: control, unburned site (hereafter UB) was established in an adjacent *P. pinaster* forest unaffected by fire at least in the preceding 40 years (dominant trees of approximately 40-cm diameter). Moderate fire severity site (hereafter MFS) had all pine crowns and upper barks burned. Here, the soil organic matter was not consumed and the ground surface remained intact after the fire. The soil was darkened and water repellent. The high fire severity site (hereafter HFS) had pines, canopy and understory litter totally burned and the entire humic soil organic layer...
consumed For HFS, the loss of soil structure was very evident and the rootlets were consumed. We devoted our greatest effort to select sites differing in fire severity but similar in terms of vegetation and local topography, aiming to avoid obvious major variation between sampling sites (Dias et al., 2010). That is, we aimed to select sites such that observed differences between them could be linked to differences in fire intensity.

In mid-June 2009, uniform areas were sampled within the three above mentioned sites. A total of 15 intact soil blocks (22 x 22 x 20 cm), five per site, were extracted randomly with a minimum spacing of 100 m with a metal cube with a sharpened edge at HSF, MSF and adjacent UB sites. This minimum distance between sampling points was chosen in order to ensure low autocorrelation and provide estimates as independent from each other as possible (Lilleskov et al., 2004, Dias et al., 2010). That is, we aimed to select sites such that observed differences between them could be linked to differences in fire intensity.

Statistical analysis

One and two-way repeated measures ANOVA were applied to explore the influence that different fire damage levels (UB, MFS and HFS) and root section parts (upper and lower) had on the response variables (morphometric traits, mycorrhizal colonization and soil chemical characteristics). Non-independence of errors between seedlings grown in the same pot was accounted for by using a DCA (Detrended Correspondent Analysis) with our complete dataset. The percentage of mycorrhization per site, overall and at each of the two vertical sections, was calculated by dividing the number of mycorrhizal root tips by the total number of root tips (Brundrett et al., 1996). Shoot and root dry biomass were determined after drying the plant material at 70°C for 48 h. in a drying oven (Sousa et al., 2011). Root/shoot ratio was derived from these measurements (Palfner et al., 2008).

Results

Plant development

Mortality rates were low and did not affect more than three plants per container. Seedlings grown in high
The proportion of total mycorrhization from both post-fire sites was significantly lower than that from undisturbed soils (HSF, P=0.006; MSF P=0.005). Regarding the two vertical sections of the root system, higher levels of mycorrhization (P<0.01) were observed in the upper (0-10cm) section compared to the lower one (>10 cm) for all three sites (Figure 3). At the upper severity fire soils (HSF) had heavier and longer shoots (P < 0.01 and P=0.030, respectively; Figure 2) and longer roots (P=0.004) than those grown in moderate severity fire (MSF) and unburned (UB) soils (Figure 2). In turn, root length from MSF sites was also longer than that from UB sites (P=0.042). Root/shoot ratio was highest for HSF and MSF sites and lowest for UB samples (HSF vs MSF P=0.798; HSF vs UB P=0.0000; MSF vs UB P=0.0001) (Figure 2).

### Mycorrhization and soil chemistry

The proportion of total mycorrhization from both post-fire sites was significantly lower than that from undisturbed soils (HSF, P=0.006; MSF P=0.005). Regarding the two vertical sections of the root system, higher levels of mycorrhization (P<0.01) were observed in the upper (0-10cm) section compared to the lower one (>10 cm) for all three sites (Figure 3). At the upper
Discussion

We found a higher mycorrhization rate for seedlings grown in unburned soils across all root sections, thus supporting our prior expectations on the negative relationship between fire severity and ECM propagules. Nonetheless, higher mycorrhization rates were unexpectedly not correlated with seedling size. In the following sections we discuss our results in the light of plant, fungi and soil features as well as their interactions, notwithstanding potentially confounding factors.

Plant development

Seedlings in the high severity fire soil showed higher shoot height, root length and root/shoot ratio and also more than 10% of the shoot biomass of those growing in unburned soil. Similar biometric results have been found by Pausas et al. (2003) in Pinus halepensis Mill. seedlings in eastern Iberian Peninsula under three fire severity classes, where seedlings from sites most affected by fire grew significantly more. Those differences may lie in the changes in soil chemistry caused by different fire severities and leading to higher fertility (see below) (Pausas et al., 2003).

Figure 4. Ordination diagram of Principal Component Analysis (PCA) performed on mycorrhizal presence on and vegetative traits of bioassay Pinus pinaster seedlings (n=75) as well as soil chemical properties. Soils were sampled after a forest fire at 1, Unburned (UB); 2, Moderate severity fire (MSF) and 3, High severity fire (HFS) sites. The Axis 1 (F1) and Axis 2 (values in brackets) explain the percentage variation of the samples according to (normalized) principal component scores. Arrows indicate the projection of a multidimensional set of axes onto a two-dimensional plane. These arrows are standardized to be of unit length, projected onto a plane. The ones that lie most closely within that plane appear longer than the ones that are more orthogonal to it. Ectomycorrhization % (M-T: Total; M-10: 0-10 cm; M-20: 10-20 cm); soil chemical characteristics (see Table 1); morphometric traits (SB: shoot biomass in gr; RL: root length in cm; R/S: root to shoot ratio).
Mycorrhization and plant development

Maximum ECM colonization rate was found in soils from unburned sites, although it did not vary significantly among high and moderate severity fire sites. Our results are in agreement with a large body of research on Mediterranean dry forests (de Román & Miguel, 2006b, Buscardo et al., 2010, Hernández-Rodríguez et al., 2013) and specifically with some studies conducted also with *P. pinaster* (Buscardo et al., 2011, Gassibe et al., 2011, Sousa et al., 2014). Nonetheless, the overall evidence in this field cannot be considered as conclusive yet. For example, Rincón & Pueyo (2010) found that fungal richness and colonization of *P. pinaster* seedlings did not depend on fire severity, but on time elapsed after fire. Indeed, time span after fire seems to mediate the evolution of fungal communities, from fire-adapted taxa to later-stage ones (Rincón et al., 2014).

Regarding the relationship between vertical root distribution (upper and lower sections) and mycorrhization rate, our results revealed how the upper part of the roots had the highest ECM rates across all fire damage levels (Visser, 1995, Torres & Honrubia, 1997). In fact, differences between upper and lower root parts across fire damage levels were kept constant (Figure 3). This was true also in the site most severely affected by fire, where higher colonization rates would have been expected at the lower (deeper) root parts. This could have come as a result of higher exposure of the top layer to very high temperatures and buffering of the lower layer (Bastias et al., 2006, Kipfer et al., 2010). Our results might indicate a particularly high resistance of some kind of propagules to fire. Here, molecular taxonomy techniques can reveal the existence of interesting pyrophytic taxa (Rincón et al., 2014).

Our experimental design did not allow separating root physiological or anatomical effects from those derived from propagule abundance or soil properties at the two depth levels within sites. For example, seedling root distribution and length varies according to soil depth (Wallander et al., 2004), in this sense post-fire seedlings tend to extend their root system vertically as seen in our results by increasing mainly taproot length therefore also changing the distribution and structure of the lateral roots (Palfner et al., 2008). Also the mycelium of ECM fungi which is usually most abundant in the superficial organic soil layers in undisturbed ecosystems (Visser, 1995, Neville et al., 2002, Wallander et al., 2004) may influence root morphology and architecture through the formation of short lateral roots and root tips (Ostonen et al., 2009, Kubisch et al., 2015), therefore affecting seedling growth (Jones et al., 2003). There is also evidence of the stratification of fungal communities (Dickie et al., 2002, Rosling et al., 2003; Anderson et al., 2007) between the 0–10 and 10–20 cm sections of soil profile, but is not always the case as reported by Anderson et al. (2007) where non stratified homogeneous ECM communities were present within the 20 cm of soil depth after two years after fire.

Nonetheless, data from our unburned site provide a suitable baseline against which we can compare the two other scenarios. The higher mycorrhization rate in the top layer of UB plant roots might be related to either root physiology or propagule abundance. Lower

### Table 2. Pearson’s correlation coefficients between ECM colonization, soil and morphometric variables affected by fire severity

| Variables | M-10 | M-20 | M-T | R/S | SB | SH | RL | Sev | pH | Cond | N | P | OM | Ca | K | Mg | CEC |
|-----------|------|------|-----|-----|----|----|----|-----|----|------|---|---|----|----|---|----|-----|
| M-10      | 1    |      |     |     |    |    |    |     |    |      |   |   |     |    |   |     |      |
| M-20      | 0.291| 1    |     |     |    |    |    |     |    |      |   |   |     |    |   |     |      |
| M-T       | 0.658| 0.664| 1   |     |    |    |    |     |    |      |   |   |     |    |   |     |      |
| R/S       | -0.181| -0.172| -0.163| 1 |    |    |    |     |    |      |   |   |     |    |   |     |      |
| SB        | -0.163| -0.085| 0.039| -0.064| 1 | | | | | | | | | | | |
| SH        | 0.091| -0.005| 0.246| -0.171| 0.657| 1 | | | | | | | | | | |
| RL        | 0.091| -0.005| 0.246| -0.171| 0.657| 1 | | | | | | | | | | |
| Sev       | -0.237| -0.271| -0.054| 0.434| 0.430| 0.245| 0.245| 1 | | | | | | | | |
| pH        | -0.323| -0.204| -0.210| 0.440| 0.124| -0.033| -0.033| 0.616| 1 | | | | | | | |
| Cond      | -0.317| -0.259| -0.159| 0.486| 0.283| 0.096| 0.096| 0.866| 0.927| 1 | | | | | | |
| N         | 0.317| 0.259| 0.159| -0.486| -0.283| -0.096| -0.096| -0.866| -0.927| -1.000| 1 | | | | |
| P         | -0.239| -0.272| -0.057| 0.436| 0.428| 0.242| 0.242| 1.000| 0.625| 0.872| 0.872| 1 | | | |
| OM        | 0.326| 0.220| 0.200| -0.458| -0.165| 0.001| 0.001| -0.686| -0.996| -0.956| -0.695| 1 | | | |
| Ca        | 0.283| 0.275| 0.106| -0.474| -0.376| -0.183| -0.183| -0.972| -0.785| -0.960| 0.960| -0.974| 0.839| 1 | |
| K         | -0.226| -0.049| -0.224| 0.222| -0.176| -0.231| -0.231| 0.005| 0.791| 0.505| -0.505| 0.017| -0.731| -0.242| 1 |
| Mg        | -0.225| -0.047| -0.224| 0.220| -0.179| -0.233| -0.233| 0.000| 0.788| 0.500| -0.500| 0.012| -0.728| -0.237| 1.000| 1 |
| CEC       | 0.281| 0.275| 0.103| -0.472| -0.380| -0.187| -0.187| -0.975| -0.776| -0.956| 0.956| -0.977| 0.831| 1.000| -0.229| -0.224| 1 |

Note: significant Pearson correlations are highlighted in black P <0.05. Where M-10: ECM % 0-10 cm; M-20: ECM % 10-20 cm; M-T: ECM % Total; R/S: root to shoot ratio; SB: shoot biomass; SH: shoot height; RL: root length; Sev: Fire Severity; Cond: Soil Conductivity; N: Nitrogen; P: Phosphorus; OM: Organic matter; Ca: Calcium; K: Potassium; Mg: Magnesium; CEC: Cation Exchange Capacity.
mycorrhization rates in MFS and HFS in that same top layer compared to UB plants, is likely due to different soil properties. Under natural conditions, mycorrhization rates in upper layers could be even higher due to mechanisms of fungal colonization such as spore dispersion by wind or rodents, which were suppressed in our experiment. Also, the same rationale applies to the lower layer. Studies similar to ours have also found lower fungal richness (Smith et al., 2004) or different fungal community structures (Bastias et al., 2006) in the upper 10 cm layer of soils variously affected by fire but interestingly, no trend at a depth of 10–20 cm (Bastias et al., 2006).

Considering mycorrhization rates alone, our P. pinaster seedlings attained smaller sizes in those soils where mycorrhization was highest i.e. in unburned soils. Nonetheless, given that potential mycorrhizal inoculum was confounded with soil chemistry, direct conclusions cannot be drawn. Inclusion in our study of seedlings grown on sterilized soils from the three studied sites, would have allowed measuring the effect of soil chemistry alone on plant growth. Notwithstanding, a negative effect of mycorrhization on plant growth rates under nursery conditions has been previously reported (Stenström et al., 1985, 1990, Le Tacon et al., 1992), even though global evidence does support the beneficial effect of ECM species on P. pinaster plant growth (Sousa et al., 2012).

Relationships among plant development, mycorrhization and soil chemistry

Soil nutrients and plant development

In our study, the percentage of ECM colonization was positively correlated with organic matter and N, but negatively with P soil content. Our results are in accordance with those of Dickie et al., (2006) in unburned bioassay soils with P. sylvestris L., where seedling ECM colonization was best predicted by humus percentage, N, Ca and clay content and soil cation exchange capacity from 0 to 20 cm depth. Furthermore, other authors noticed that fungal communities can adapt to more nitrogen-rich sites (Toljander et al., 2006, Kranabetter et al., 2009). Also, Sousa et al., (2011) studied 6 month-old P. pinaster seedlings grown in burned soils and inoculated with ECM fungi. These authors reported that a low N content was not a factor that limited plant growth, perhaps offset by a higher P content. Indeed increasing P availability has been related to inhibition of fungal ECM colonization (Grant et al., 2005, Smith & Read, 2008) and enhancement of plant growth (Conjeaud et al., 1996).

In our study, mycorrhizal inoculum potential appeared to be affected by soil disturbance caused by fire similar to that reported by Buscardo et al. (2010) and Sousa et al. (2011), while plant growth increased along a fire severity gradient. This was likely due to post fire nutrient deliverance in the forest soil such as P (Fierro et al., 2007) rather than ECM colonization. As we could not separate fire severity and ECM colonization effects, the latter also may have influenced the uptake of P (de Lucia et al., 1997), but likely to a lesser degree due to the strong fire effect (Turrión et al., 2010). Regardless of the limitations, bioassay studies like ours can be a useful tool when studying ectomycorrhizal infectivity and may be comparable to some field situations (Izzo et al., 2006). Particularly, they can provide insight about background mycorrhization levels in seedlings emerged after a fire and whether artificial mycorrhization can improve plant growth in those situations (Sousa et al., 2011). Also, bioassay studies provide valuable information on seedling performance, which is the main goal of afforestation practices, even more after disturbing events like wildfires.

All this suggests that integrative approaches that combine laboratory and field experiments (Buscardo et al., 2011) are needed to assess ECM functioning in ecosystems dominated by Mediterranean pyrophitic species such as P. pinaster, aiming to achieve a successful restoration of Mediterranean forest areas affected by wildfire.
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