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Linkages between climate, seasonal wood formation and mycorrhizal mushroom yields

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ABSTRACT

Fungi provide important forest ecosystem services worldwide. In Mediterranean pine forests, predicted warmer and drier conditions could lead to a decline in mushroom yields. Climate is a key factor regulating both tree growth and fungal yields, particularly in drought-prone Mediterranean ecosystems. However, the responses of forest growth and mushroom production to climate depend on the differences among tree and fungal species and functional groups (e.g., mycorrhizal *vs.* saprotrophic), forest types, as well as depending on site conditions. Here we investigate how climatic conditions drive seasonal wood formation (earlywood –EW– and latewood –LW– production) and mycorrhizal mushroom production, to disentangle if growth and fungal yields are related. This assessment was done in Mediterranean forests dominated by four pine species in two areas located in Catalonia (NE Spain) representing mesic and xeric conditions and encompassing wide ecological gradients. The data consisted of 7-year to 13-year long inventories of mushroom production. EW production was favoured by cold and wet climate conditions during the previous fall and winter, and during the current spring and summer. LW production was enhanced by warm and humid conditions from spring to early fall. Mushroom yield was improved by wet late-summer and fall conditions, mainly in the most xeric area. This study confirms the ample differences found in tree growth and fungal production along ecological and climatic gradients. Clear relationships between mycorrhizal fungal yields and tree growth were mostly observed in specific sites characterized by severe summer drought. Specifically, latewood production seems to be the tree-ring variable most tightly linked to mycorrhizal fungal yield in drought-prone areas.

1. Introduction

Climate plays a major role on the production and diversity of fungal communities, being precipitation, temperature and moisture key drivers for mushroom fruiting (Boddy et al., 2014; Pinna et al., 2010). In temperate and boreal forests, delayed fungal fruiting in fall or decreased fungal yield have been generally related to warmer and drier years, respectively (Kauserud et al., 2008; Diez et al., 2013). In Mediterranean pine forests, reduced mushroom yields usually correspond to more severe dryness during summer and autumn (Ágreda et al., 2015; Büntgen et al., 2015). Contrastingly, there is evidence of longer fruiting season and increased fungal production in temperate Central European forests due to rising temperatures (Büntgen et al., 2012, 2013). These diverse find-

Abbreviations: PS, *Pinus sylvestris*; PN, *Pinus nigra*; PH, *Pinus halepensis*; PP, *Pinus pinaster*; EW, earlywood width; LW, latewood width; DBH, diameter at breast height; PET, potential evapotranspiration rate; P, precipitation; MFY, mycorrhizal fungi yield; CV, coefficient of variation.

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ings suggest that fungal yields are differently driven by climate depending on local site conditions (e.g., topography, soil properties) and forest stand dynamics (e.g., basal area, tree growth, Bonet et al., 2012, 2010, 2004; de-Miguel et al., 2014; Martínez-Peña et al., 2012; Tahvanainen et al., 2016). Nevertheless, when investigating fungal production as related to climate and forest growth, clear trends and associations between these three components are rarely observed, probably because of differences between functional fungal groups, forest types, climatic conditions and methodological issues affecting fungal records (Boddy et al., 2014).

The symbiotic associations formed by mycorrhizal fungi with tree roots enhance the transfer of soil nutrients to trees, while organic carbon compounds fixed by trees are derived to fungi (Gerdemann, 1970). The phenology and photosynthetic activity of the host tree and its response to climate may also influence differently mycorrhizal and saprotrophic fungal fruiting arising from their differential dependence on climate conditions (Boddy et al., 2014). Additionally, the sensitivity of mycorrhizal fungi to climate may depend on the tree-fungi associations and the strength of those relationships (e.g. deciduous *vs*. coniferous tree species, Gange et al., 2007). Nevertheless, links between the type of tree host species and the phenology of mushroom fruiting have been detected in some cases (Dickie et al., 2010) whilst in others no association has been found (Pinna et al., 2010).

Tree radial growth may be used as a proxy of carbon availability to trees since wood formation has a low allocation priority compared to shoot development (Fritts, 2001). The study of tree-ring features for ecological purposes (dendroecology) is therefore a powerful tool to understand how coupled long-term climatic conditions, forest growth, and mushroom production are (Büntgen and Egli, 2014). Mycorrhizal fungal production has been indeed associated with tree growth in thinning experiments (Egli et al., 2010). However, since the production of mushroom fruiting bodies is apparently highly dependent on current photosynthates (Högberg et al., 2008), mycorrhizal mushroom yield could be related to seasonal wood production as, in conifers, the latewood is mostly formed by current-year photoassimilates, while the earlywood contains carbohydrates synthesized from the previous summer and fall and current spring (Kagawa et al., 2006). Therefore, observational studies aiming to relate climate, wood and mycorrhizal fungal production should consider the main climatic constraints of tree growth and fungal fruiting, and the phenological patterns of both processes which are linked to carbon synthesis and use within the tree. For example, these studies should consider that both mycorrhizal mushroom production and latewood formation usually peak during summer and autumn in most conifers of the Northern Hemisphere and therefore, these two variables could be coupled to some degree.

In this framework, we propose assessing the potential of tree rings to investigate the long-term relationships between climate conditions, seasonal wood formation (earlywood and latewood widths), and mycorrhizal mushroom production. We argue that mycorrhizal and saprotrophic fungal production during fall, when maximum yields are recorded in the Northern Hemisphere, must be separately considered based on their different dependence on climate (Egli et al., 2010). Our main objectives are (1) to determine the main climate variables influencing seasonal wood formation and mycorrhizal fungal productions, and (2) to analyse whether the production of mycorrhizal fungi is related to earlywood and latewood production. Our working hypothesis are that: (1) earlywood formation will be influenced by spring climatic conditions whilst latewood formation will be more dependent on late-summer and fall climate; (2) annual mycorrhizal fungi yields will be mainly influenced by late-summer and fall climate conditions, when fungi fruiting peaks; (3) the influence of water availability on both wood (earlywood and latewood widths) and mycorrhizal mushroom production will be stronger in the most xeric sites; and (4) latewood width, and not earlywood production, will be related to mycorrhizal fungi yield as a function of late summer to fall climatic conditions.

2. Material and methods

2.1. Study area

The study was conducted in monospecific stands of the most common pine forest ecosystems found in Catalonia, NE Spain (*Pinus sylvestris* L., *Pinus nigra* J.F. Arnold, *Pinus halepensis* Mill. and *Pinus pinaster* Ait.). We selected two areas subjected to different climatic conditions (Solsonès and Prades) for sampling (Fig. 1). The plots in Solsonès area corresponded to natural stands, whereas the Prades plots were placed on pine plantations established in the 1960s. Of the total of 107 permanent plots currently monitored for the annual mushroom yield estimation (de-Miguel et al., 2014), we sampled nineteen stands (13 stands in Solsonès and 6 stands in Prades) located between 530 and 1502 m a.s.l., corresponding to highly productive fungal areas (Table 1). Therefore, total mushroom yields from the selected sample plots need to be considered with care inasmuch as they may not be necessarily representative of the expected productivity of a typical forest stand.

The Solsonès area is subjected to continental and sub-Mediterranean conditions, with a mean annual temperature of 11.1 °C and a mean annual precipitation of 726 mm, whereas the Prades area experiences a stronger Mediterranean influence, i.e. a more intense drought stress during the growing season (mean annual temperature of 12.1 °C and mean annual precipitation of 564 mm). For each plot, physiographic and stand attributes such as slope, aspect, elevation, tree density and basal area were also recorded (cf. Table 1).

2.2. Data collection

2.2.1. Dendrochronological methods

Around each plot where mushroom production was assessed, 10–15 dominant trees were randomly selected for sampling in late 2014 and early 2015 in an area *ca*. 0.5-ha large. Two radial cores per tree were extracted at 1.3 m above the ground level using a Pressler increment borer. The cores were air-dried, mounted on wood boards, and polished with sandpaper grits until rings were clearly visible. The wood samples were visually cross-dated. Then, earlywood (EW) and latewood (LW) widths were separately measured to the nearest 0.01 mm using a stereomicroscope and a Lintab sliding-stage measuring device in conjunction with TSAP-WinTM software (F. Rinn, Heidelberg, Germany). EW and LW were visually distinguished based on the different lumen area and cell-wall thickness of the tracheids forming each type of wood. Cross-dating was verified using the COFECHA program (Holmes, 1983). We obtained chronologies of EW and LW widths for each plot by averaging the values for each year across the trees sampled within each plot. For each tree, we measured the diameter at breast height (DBH) and estimated the age at 1.3 m by counting the number of rings of the oldest core containing the pith or showing the innermost curved rings indicating proximity to the pith.

2.2.2. Mushroom yield assessments

Mushroom sampling started in 1997 in Solsonès plots, and in 2008 in Prades plots. From 2002–2006, sampling was not carried out. Mushroom production (fresh mass) and species richness were inventoried every week from September to December in squared plots (10 m x 10 m), when most fungi fruiting occurs (Bonet et al., 2012; Martínez de Aragón et al., 2007), and the collection included