Forest Ecology and Management 258 (2009) 2511–2518

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Changes in the spatial structure of oak carbon-based secondary compounds after pine harvesting

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ARTICLE INFO

Article history:
Received 7 July 2009
Received in revised form 1 September 2009
Accepted 2 September 2009

Keywords:
Forest harvest
Geostatistics
Pinus pinaster
Polyphenols
Tannins
Quercus robur
Spatial variability

ABSTRACT

In natural plant populations, leaf polyphenols show high intraspecific variation that occurs both temporally and spatially. Leaf phenolics may be induced by diverse ecological factors such as light, nitrogen availability or herbivory attack. Both light and nitrogen availability can show spatial structure in forested stands, meaning that they each have a high degree of autocorrelation, which can determine the appearance of spatial structure in leaf polyphenols. However, the availability of these resources may be drastically changed by forest disturbance, and little is known about the effect of forest disturbance on the spatial pattern and scale of leaf secondary compounds. We hypothesise that the spatial structure of leaf polyphenols in understory vegetation will disappear due to forest harvesting, because these compounds depend on light availability, yet it will remain unaltered for those compounds that either depend on the availability of other resources or are under major genetic control. The study was performed in young pedunculate oak (*Quercus robur*) populations growing either under a pine canopy (*Pinus pinaster*) stand or in a pine harvested stand in NW Spain. The spatial structures of green and senescent leaf polyphenols, tannins, non-tannin polyphenols and nitrogen were analysed in both stands using geostatistical analysis. The spatial structures observed for green and senescent leaf polyphenols and tannins in the forested stand disappeared in the harvested stand. However, non-tannin polyphenols, as well as nitrogen, showed spatial structure in both stands. Understanding these changes may be important for the successful recovery of native oak populations growing under pine forests in NW Spain, one of the priorities of the local government. Our results showed that changes in the concentration of leaf secondary compounds after disturbance may be accompanied by differences in their spatial properties, which may have important consequences for ecosystem function.

1. Introduction

Polyphenols represent a diverse group of plant secondary compounds that affect a number of ecological processes controlling forest dynamics. Leaf phenolics may influence the susceptibility of plants to herbivore attack and pathogen infection, and they may also influence foraging behaviour and the development of insects and parasites (Karban et al., 1997; Agrawal and Karban, 1999; Dolch and Tscharntke, 2000). Polyphenols have also been recognised as regulators of soil processes. Through their effects on the activity of soil organisms and their physico-chemical effects on the pools and forms of nutrients, phenols reduce the turnover of organic matter and mineralisation rates, shifting N cycling from mineral to organic-dominated pathways (Northup et al., 1995, 1998; Schimel et al., 1998; Hättenschwiler and Vitousek, 2000; Kraus et al., 2003). Therefore, the pattern of phenotypic variation in plant polyphenols has been recognised as an important factor in understanding the coevolutionary interactions of plants and herbivores, competitive plant relations and community structure (Northup et al., 1999; Hodge, 2004; Brenes-Arguedas and Coley, 2005; Andrew et al., 2007).

The production of polyphenols in leaves is partly under genetic control and partly determined by environmental conditions (Waterman and Mole, 1989; Berenbaun and Zangerl, 1992; Herms and Mattson, 1992). The spatial pattern of leaf phenolics may be induced by diverse ecological factors. Light is probably the most important factor explaining carbon-based metabolite content, and its availability is especially important for understory vegetation, where light intensity is spatially and temporally diverse (Baldocchi and Collineau, 1994; Dudt and Shure, 1994; Pearcy and Sims, 1994). Nutrient availability, specifically nitrogen, may influence polyphenol concentration as well (Koricheva et al., 1998; Haukioja et al., 1998; Keinänen et al., 1999).

Indices of light and nitrogen availability frequently show spatial autocorrelation in natural ecosystems (Jackson and Caldwell,

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doi:10.1016/j.foreco.2009.09.007

1993; Schlesinger et al., 1996; Nicotra et al., 1999) and they may induce a spatial pattern of leaf phenolic concentrations (Covelo and Gallardo, 2004). These authors found significant correlations and the same spatial patch scale between total leaf phenolic content and both radiation beneath the canopy and leaf N content in oaks under the canopy of mature *Pinus pinaster* stands.

Oak foliar phenols also vary in response to disturbance regimes (Dudt and Shure, 1994; Covelo and Gallardo, 2001). Disturbances alter the availability and distribution of plant resources, and their influence on spatial patterns of variability in plant populations can vary, depending on the interaction among frequency, extent and intensity of disturbance (Fraterrigo and Rusak, 2008). However, little information is available on changes in the spatial structure of leaf secondary compounds with disturbance and whether this spatial structure differentially affects different secondary compounds. In *P. pinaster* stands in the north-western region of the Iberian Peninsula, pines are periodically harvested, increasing light availability for young oak saplings and leading to a reduction in organic matter and nutrients in the soil, changes that are associated with increased erosive processes (Merino et al., 1998; Covelo and Gallardo, 2002). Thus, we hypothesised that the spatial structure of leaf secondary compounds (total phenols, tannins, and non-tannin phenols) in forested stands would disappear in harvested stands for those secondary compounds that strongly depend on light availability. The tannin:N ratio was also considered due to its influence on the efficiency of conversion of digested matter to body mass by herbivories (Barbehenn et al. (2009). Complementarily, the spatial structure of leaf secondary compounds would remain unaltered for those compounds that either depend on the availability of other resources or are under major genetic control. We also expected that leaf senescence would decrease the spatial structure of leaf polyphenols because multiple physiological mechanisms are involved in leaf senescence (e.g., increases in polymerisation and binding to cell walls), adding noise to the former spatial structure detected in green leaves.

2. Methods

2.1. Study site

The study was conducted in a 30-year-old maritime pine forest (*P. pinaster* Aiton) in north-western Spain (42°10′N, 08°40′W). The site was located 450 m above sea level, near the University of Vigo campus. Pine density was ca. 400 trees per hectare, with an average pine height of 15 m. Leaf area index and canopy openness (as estimated by hemispherical photograph) ranged from 1.67 to 2.15 and 17.1% to 19.5%, respectively. The stratum under the pine canopy largely comprised young (ca. 10–15 years old) deciduous oaks (*Quercus robur* L.), with the occasional presence of *Castanea sativa* Mill. Bracken fern (*Pteridium aquilinum* (L.) Kuhn) and *Agrostis curtisii* Kerguelen dominated the herbaceous stratum. The climate is warm-temperate with a slight Mediterranean influence, with little rainfall during the summer months. Mean annual rainfall is about 1800 mm, and the mean annual temperature is about 15 °C. Soils (classified as Humic Cambisol) are acidic (pH 4.3–4.7) and derived from the weathering of gneiss bedrock (IGME, 1981).

2.2. Field sampling

The study area has been part of a soil and plant monitoring project since the spring of 1995. The pine canopy covered the complete area until the summer of 1995. Approximately 50% of this area was harvested by the end of the summer, leaving the young oaks (ca. 10–15 years of age and from 2 to 3 m tall) as the dominant tree species.

Two randomly selected plots were chosen from within the forested and harvested sites with an area of about 120 m × 120 m and 80 m × 80 m, respectively. Furthermore, an irregular plot was marked inside these areas to leave out apparently disturbed surfaces (affected by roadways or forestry works) and include a buffer zone (ca. 10 m) separating the plot from these disturbed zones. All young oak trees in the plots ($n = 125$ and $n = 93$ at forested and harvested areas, respectively) were tagged and mapped using the computer program INTERPN, based on tree diameter and tree-to-tree distance measurements (Boose et al., 1998). Mean and minimum distances between trees were 4.4 and 1.1 m and 5.5 and 0.8 m at the forested and harvested site, respectively (Fig. 1). Green and senescent leaves were sampled during August 2006 and December 2006, respectively. Senescent leaves were taken when they had already suffered the abscission, just prior to leaf fall (leaves that fell from the tree with just a gentle shake or touch). These leaves were collected directly from trees rather than from leaf litter to ensure sampling of fresh abscised leaves and also to avoid soil contamination. At each tree, about 20–25 leaves from different positions were picked. Leaves were

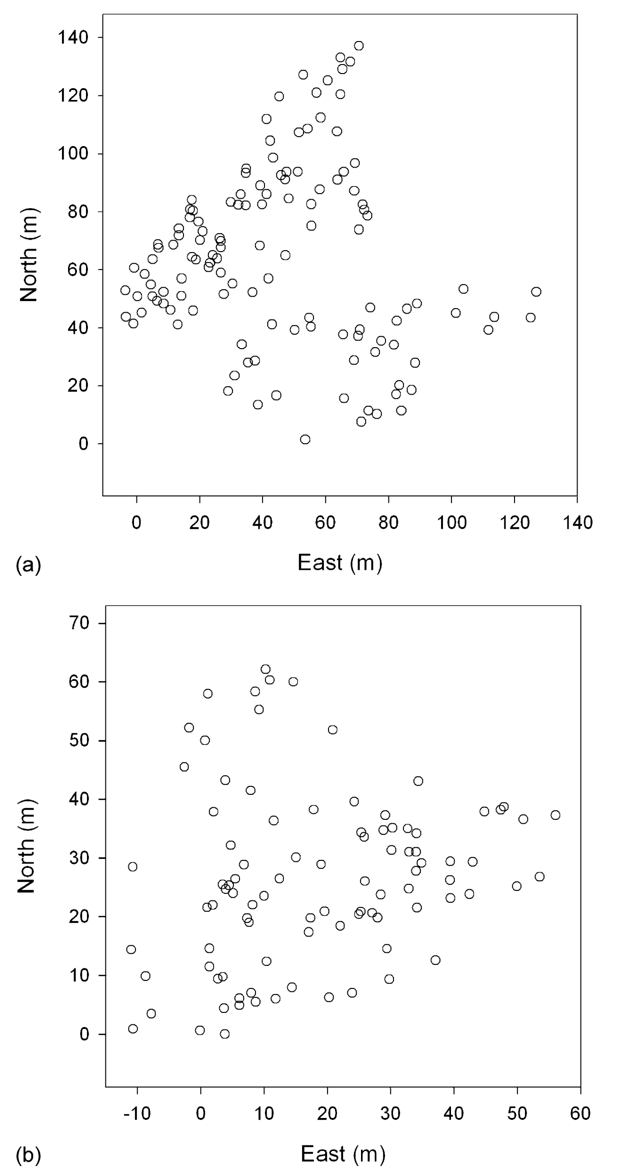

Fig. 1. Diagrams of young oak tree locations in the understory of the (a) forested and (b) harvested *Pinus pinaster* stands.