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Growth patterns at the southern range edge of Scots pine: Disentangling the effects of drought and defoliation by the pine processionary caterpillar

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ABSTRACT

Dendrochronology and climate-growth modelling were used to assess to what extent defoliation by pine processionary moth (*Thaumetopoea pityocampa*) depresses growth in Scots pine (*Pinus sylvestris*) at the species' southernmost distribution limit (southern Spain). Basal area increment (BAI) was measured in severely defoliated and non-defoliated trees, for a period of 20 years, a period that includes three severe droughts and two severe outbreaks of pine processionary moth. Linear mixed-effects models of BAI as a function of climate were run for non-defoliated trees and thereafter the fit of the model was tested separately both for defoliated and non-defoliated ones. Severely defoliated trees showed pronounced growth reductions during defoliation, although their cumulative basal area and drought-sensitivity were similar to those of non-defoliated trees. The results were not related to tree size or age, while non-climatic residuals were significantly related to the defoliation percentage. The combined effect of drought stress and processionary caterpillar defoliation caused short-term growth reduction in affected trees, although defoliated trees presented higher growth recovery after the defoliation, displaying similar average growth. We conclude that, in Scots pine, the growth reduction induced by processionary caterpillar defoliation can be overcome to a greater extent than the impact of drought.

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1. Introduction

Wood is a main terrestrial ecosystem carbon sink (Hyvönen et al., 2007), therefore a given factor with positive net effects on tree growth may increase forests ability to down-regulate carbon atmospheric levels, whereas factors negatively affecting tree growth may boost C sources (Logan et al., 2003; Canadell and Raupach, 2008). Biomass gain can be altered through disturbances, such as severe defoliations by herbivorous insects. As ectotherms, phytophagous insects can also benefit from rising temperatures and could constitute a predisposing tree-decline factor by increasing herbivore damage. Severe loss in leaf area may weaken defoliated trees by, for instance, depressing tree growth after leaf loss (Netherer and Schopf, 2010). Furthermore, global warming may have contrasting effects on herbivorous insect-tree interactions, driving declining tree growth and vigour after severe defoliations and thereby leading to potential vegetation shifts over large geographical areas, with major impacts on ecosystem function (Galiano et al., 2010).

In addition, global warming might also promote the expansion of some herbivore species that have distribution areas limited mainly by low temperatures (Shaver et al., 2000; Logan et al., 2003; Björkman et al., 2011). The response to co-occurrence of warming and defoliation should not be predictable from single-factor analyses, as a combination of stressors can result in intensification, overlapping or amelioration of the effects of stress (Quentin et al., 2012; Bansal et al., 2013). Such effects will likely be more pronounced in water-limited populations, as tree growth is drought sensitive and leaf-area recovery after defoliation is water-and nutrient-consuming, leading to lower growth rates on defoliated trees (Pinkard et al., 2011). To investigate these points, we chose a Scots pine (*Pinus sylvestris* L.) population affected by severe defoliations by the pine processionary moth *Thaumetopoea pityocampa* (Denis and Schiffermüller; Lepidoptera: Notodontidae), at the southernmost distribution limit of this species, where water availability should be the main growth-limiting factor (Matías and Jump, 2012; Sánchez-Salguero et al., 2012; but see also Herrero et al., 2013).

The pine processionary moth is a major pest of *Pinus* and *Cedrus* trees in the Mediterranean area (Netherer and Schopf, 2010). *T. pityocampa* presents episodic events of defoliation during which

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extensive areas are massively defoliated. In southern Spain the incidence of these outbreaks is significantly related to climatic conditions (Démolin, 1969; Hódar and Zamora, 2004; Hódar et al., 2012). Among abiotic factors, temperature appears to be key in regulating this insect's performance. Thus, at high altitudes, where low temperature is likely limiting, outbreaks should be favoured by mild winters, while in lowland stands higher temperatures would encourage a more stable outbreak pattern, constrained by predators and parasitoid dynamics (Hódar et al., 2012). Furthermore, there is a trend towards reduced herbivory in plants adapted to low-resource environments (Coley et al., 1985), as should be the case of Mediterranean high mountains (Castro et al., 2004). Therefore, both abiotic and biotic factors drive the range shift and outbreak development of the pine processionary moth (Hódar and Zamora, 2004; Battisti et al., 2005, 2006; Hoch et al., 2009). However, warming-induced pine processionary moth displacements, upwards in mountains and northwards in latitude, are promoting the encounter of this herbivore with new pine populations and/or species which were outside its range until now, such as dwarf mountain pine (*Pinus mugo*) in the Alps, and Scots pine in many other parts of Europe (Hódar and Zamora, 2004; Battisti et al., 2005, 2006).

The establishment and reinforcement of the interaction between the pine processionary moth and Scots pine is of special interest, as this pine is the conifer with the widest geographical distribution area in the world (Gausen et al., 1964), being a particularly important forestry species in economic and ecological terms (Kuper, 1994; Archibold, 1995). The current core of Scots pine range is located in the central and northern parts of Europe and Asia, while it is restricted to Mediterranean high-mountain relict populations in southern Europe (Robledo-Arnuncio et al., 2009; Matías and Jump, 2012). The southernmost populations of the species are today restricted to the Sierra Nevada range, SE Spain, where several factors hamper regeneration, such as high rates of seed predation (Castro et al., 1999), seedling mortality due to summer drought (Castro et al., 2004), and high pressure from ungulate herbivory (Gómez et al., 2001; Zamora et al., 2001). For adult trees, the main problem is their own persistence in a Mediterranean environment in which they are forced to survive under severe summer-drought conditions. Although these southernmost Scots pines appear to have developed some local adaptations to harsh conditions (Alía et al., 2001; Herrero et al., 2013), increasing defoliations by the pine processionary moth could threaten the future of these relict populations (Hódar et al., 2003; Hódar and Zamora, 2004).

Defoliation by pine processionary moth may be considered a single or episodic event that disrupts the current growth conditions and results in total or partial destruction of the tree's foliar biomass, while drought acts as a sustained deviation from average water availability that causes reduced growth rates. When defoliation and drought occur simultaneously, their interactive effects on plant performance could be additive (responses were equal to the sum of the single-factor effects), synergistic (greater than expected) or antagonistic (less than expected) on tree growth (Bansal et al., 2013). Here, we hypothesise that trees affected by defoliation should be more drought-sensitive (i.e. drought-induced growth reduction will be higher than expected, compared to non-defoliated trees). To test this hypothesis we use dendrochronology to retrospectively assess changes in basal area increment in Scots pines free from and affected by the pine processionary moth at the southern margin of *P. sylvestris* distribution area.

2. Materials and methods

2.1. Study area and field sampling

The study area includes the southernmost natural Scots pine forests, located in the Sierra Nevada National Park (south Spain; Electronic Supplementary material, Fig. S1). Based on extensive field surveys, we selected a Scots pine stand at 1650 m a.s.l., (37°05′N, 3°28′W). The area has a continental Mediterranean climate, with cold winters and hot, dry summers. The mean minimum temperature in the coldest month (January) is 1.1 °C, and the mean maximum of the hottest month (July) is 29.2 °C. The mean total annual rainfall is 811 mm, concentrated during winter, spring and autumn; 4% of the total annual rainfall is registered in summer (data from La Cortijuela Botanical Garden, about 2 km from the study area; see also Electronic Supplementary material, Fig. S2). The natural vegetation is dominated by native Scots pines *P. sylvestris* var. *nevadensis*, junipers (*Juniperus sabina* L., J. *communis* L.) and shrubby species (e.g. *Berberis vulgaris* L.). Patches of natural vegetation are intermingled with pine plantations from the 1960s and 1970s with variable combinations of Scots (*P. sylvestris* var. *iberica*) and Black pine (*P. nigra*). Plantations were made at high densities (1500–2000 trees/ha), but a forest fire in early 1980s and clearing works in 2000 reduced the density to 500 trees/ha. The bedrock is calcareous and the predominant soils are regosols and cambisols, shallow with a basic pH (Castro et al., 2004).

In 1998, for three consecutive winters (1998–2000) the area underwent an explosive pine processionary moth outbreak. At the beginning of the outbreak, we selected 82 adult *P. sylvestris* trees in a 35-year-old plantation, most of them belonging to the var. *iberica*. All trees were adult, reproductive, and isolated or at the border of stands. This selection criteria was chosen based on known preference of pine processionary moth for stand borders, generally rejecting dense stands; furthermore, it reduced the effect of competition by conspecific trees. Trees were labelled irrespective of their degree of defoliation, although in that year most of them were severely defoliated. From that time on, the trees were visited at the end of each winter (March–April), as defoliation finishes at this time and the larvae descend to the soil for pupation, and defoliation percentage was visually estimated in two perpendicular views of the tree. All the estimations were made by the same observer (JAH). Four trees died during the 10 years following the initial labelling, all of them pines belonging to the severely defoliated group during the first outbreak, thus leaving a final sample of 78 trees.

In May 2009, after the check for the winter of 2009, we ranked the 78 live trees according to the defoliation undergone during the previous 12 years. This period included two pest outbreaks, the very severe one at the beginning of the study, and other rather mild one in 2004–2005, and a third outbreak was starting. After the ranking, we selected the trees that had never been defoliated by more than 50% and with an average defoliation of below 10% for the 12 years, and trees with at least two defoliations exceeding 90% and averaging more than 20%; 29 and 21 trees, respectively, met these criteria. In order to homogenize the origin and condition of the trees used for analysis, from these groups we discarded pines coming from spontaneous regeneration (14), living in rocky soils (2), damaged by other herbivores or by abiotic conditions (wind, frost) (4), and those close to another pine already sampled (the rest). This left us finally with two groups of 12 pines, hereafter labelled as non-defoliated trees (mean % defoliation ± SE 3.8 ± 0.5) and defoliated trees (27.0 ± 1.0), respectively. Given that the study area is relatively homogeneous in soil properties, elevation, aspect, slope, etc., and the selected trees are also very similar in age and size, we consider this number of replicates sufficient to characterize contrasting growth patterns between the two groups.

In October 2009, the 24 trees selected were sampled for the dendrochronological study. Tree height was visually estimated, and the diameter at the breast height (dbh) recorded. Average dbh was about 20–25 cm, tree height was about 7–8 m, and tree age at coring height was about 30–35 years old; no significant

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