



Pine growth response to processionary moth defoliation across a 40-year chronosequence

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ABSTRACT

Estimating the impact of pest insects on forest productivity requires a better understanding of host tree responses. While many studies have focused on juvenile trees, studying the impacts of defoliation on trees of increasing age helps to better characterize underlying mechanisms regulating growth responses to defoliation. During winter 2009–2010 a large outbreak of pine processionary moth occurred in South-western France. We established a field experiment to examine the effects of pine processionary moth defoliation varying from 25% to 100% on the growth of *Pinus pinaster* in stands ranging from 3 to 40 years old. Our results showed that pine processionary moth defoliation resulted in significant loss of radial growth for at least two years following defoliation. Stem growth loss in the first and second years was proportional to defoliation intensity and ranged from 32% to 93% in year 1, and from 17% to 68% in year 2. Stem growth was most reduced in older trees. Carbohydrates and nitrogen contents in needles and stem sapwood were also affected by defoliation. Our results suggest that defoliation affects stem growth through nitrogen and carbon resource limitation and that stem growth would be a lower priority sink for resources than other physiological processes in pine trees.

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1. Introduction

Forests are important carbon sinks worldwide (Hyvönen et al., 2007), and may help to mitigate the detrimental effects of climate change (Luyssaert et al., 2010). Thus, the maintenance of tree growth potential is crucial. However, global warming poses several risks to carbon sequestration in forests. In particular tree damage by defoliating insects is likely to be enhanced by increased temperatures (Robinet and Roques, 2010) and drought (Jactel et al., 2011), thus resulting in reduced forest productivity (Nabuurs et al., 2008). It is therefore critical to model the impact of insect defoliation on net forest primary production in order to better predict future carbon storage in the global change context.

In addition to the direct detrimental effects of defoliation on total biomass and productivity (Chen et al., 2002), insect defoliations have been shown to affect carbohydrate and biomass allocation patterns in trees (McNaughton and Chapin, 1985; Eyles et al., 2009), foliar nitrogen (N) or related protein concentrations (Piene, 1980; Caldwell et al., 1981; Wagner and Evans, 1985), photosynthetic activity (Reich et al., 1993; Turnbull et al., 2007; Quentin

et al., 2010), and defensive chemistry (Turnbull et al., 2007), all of which could further affect tree resistance to biotic and abiotic stresses.

It has been suggested that non-structural carbohydrates (NSCs), usually considered as a carbon reserve for energy and biosynthesis, mediates tree growth responses to defoliation (Eyles et al., 2009; Pinkard et al., 2011). Moderate and severe defoliation usually results in reduced NSC concentrations (Palacio et al., 2011, but not always in case of light defoliation, e.g. Van der Heyden and Stock, 1995) which might in turn reduce carbon allocation to tree growth (Trumble et al., 1993). It is also well established that a share of carbon reserves are necessary to support various vital processes such as respiration, reproduction, defense and tree growth (Mund et al., 2010; McDowell et al., 2011; Pinkard et al., 2011). However, such carbon limitation does not appear to be long lasting (Palacio et al., 2011, 2012). For example, in evergreen conifers (*Pinus cembra*), rapid replenishment of carbon stores following defoliation has been observed (Li et al., 2002; Roitto et al., 2003). These observations suggest that the impacts of defoliation on tree growth may not only or directly depend on quantitative changes in NSC concentrations. As older needles are the main storage organs for nitrogen, defoliation could also result in a significant loss of N stores (Li et al., 2002; Millard et al., 2001), which may impede stored nitrogen remobilization for photosynthetic processes and tree metabolism.

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There is therefore a lack of understanding of how trees respond to carbon and mineral constraints resulting from defoliation (Reich et al., 1993; Vanderklein and Reich, 1999; Eyles et al., 2009; Pinkard et al., 2011). The relative importance of metabolic processes and patterns of carbon and nitrogen allocation change with tree age (Mäkelä and Valentine, 2001) thus, we argue that assessing the effects of defoliation across a chronosequence of age classes may shed new light on mechanisms linking defoliation to growth loss. Kulman (1971) and Wainhouse (2005) suggest that young trees are more likely than old trees to die following severe defoliation. Young and mature conifer trees differ in the proportion of old vs. young needles (Porté et al., 2000) and these differences might influence their response to defoliation (Kelly et al., 1995; Straw et al., 2011). Larger trees are for example expected to better mitigate the effects of defoliation because they have larger stored nutrient reserves (Niinemets, 2010).

Pine processionary moth (PPM) *Thaumetopoea pityocampa* (Dennis & Schiff) is the main insect defoliator of pine and cedar species in Southern Europe (Devkota and Schmidt, 1990; Masutti and Battisti, 1990). In the last decade, its range has spread towards higher latitudes and altitudes, probably in response to rising winter temperatures (Battisti et al., 2005; Robinet et al., 2007). Mild winters are also assumed to improve larval survival and then increase PPM population level leading to more severe defoliation in the next generation of larvae. Defoliation by PPM usually results in significant growth reduction (Lemoine, 1977; Hódar et al., 2003; Kanat et al., 2005). A recent meta-analysis of tree growth responses to PPM defoliation (Jacquet et al., 2012) suggested that growth losses do not increase linearly with defoliation intensity and are higher in young than in mature trees. However, the use of different methodological approaches for determining tree growth loss and defoliation rate may have obscured the general pattern of growth response. Additionally, the effect of tree age has never been examined simultaneously with that of defoliation intensity within the same experiment.

To control for the impacts of magnitude and location of defoliations (Hjältén, 2004), artificial defoliation has often been used as a substitute for natural defoliation (Quentin et al., 2010). Artificial defoliation provides a logistically simpler approach for controlling the extent and timing of defoliation, thus allowing for the development of experimental approaches that control for both tree age and defoliation rate. However, the capacity of artificial defoliation to accurately mimic real herbivore damage (Baldwin, 1990; Hjältén, 2004), notably in terms of spatial and temporal patterns (e.g. Reich et al., 1993; Vanderklein and Reich, 1999), remains uncertain. Furthermore, physiological responses to artificial and natural defoliation may differ (Quentin et al., 2010).

PPM population dynamics shows a cyclic pattern with outbreaks occurring every 6–8 years (Battisti, 1988; Robinet, 2006). During the winter 2009–2010, we observed such an outbreak in the Landes de Gascogne Forest but with an extreme intensity since maritime pine stands of all ages were severely defoliated by the insect, some trees being 100% defoliated. We took advantage of this large biotic disturbance to set up a large field experiment where we controlled for both the age and the defoliation rate of trees to quantify the impacts of defoliation by PPM on growth dynamics in the commercially important tree species *Pinus pinaster*. More specifically our objectives were to test the following hypotheses:

- (1) Radial growth losses associated with PPM defoliation are proportional to the amount of foliage removed, by both natural and artificial defoliations.
- (2) The magnitude of PPM defoliation effects on radial growth decreases with tree age.
- (3) Growth responses to PPM defoliation are driven by carbohydrate and nutrient resources limitation.

2. Materials and methods

2.1. Study area

The study was carried out in even-aged monospecific maritime pine (*P. pinaster* Ait.) stands in the “Landes de Gascogne” forest, south-western France, the largest plantation forest in Europe with ca. 1 million ha of maritime pine. The stands were selected in a small region (5 km × 5 km) (44°44′00″N, 00°46′00″W), with very homogenous pedo-climatic conditions, located ca. 40 km south of Bordeaux. The climate of this region is thermo-Atlantic (mean annual temperature of 13 °C, mean annual precipitation of 977 mm) with wet winters and marked drought in late summer (August–September). For the two years of the study precipitation was 812 mm and 638 mm in 2010 and 2011 respectively. Monthly averaged maximum and minimum temperatures in 2010 were 28.3 °C and 0 °C respectively and 27.7 °C and 1.3 °C respectively in 2011. The region is flat with podzol soils established on several meters of sandy deposit.

2.2. Experimental design (natural defoliation)

To quantify the impacts of PPM defoliation on *P. pinaster* growth as a function of defoliation intensity and stand age, we selected 11 stands along a chronosequence spanning from 3 to 40 years old (3, 6, 9, 10, 11, 13, 18, 19, 28, 29, and 40), i.e. covering the full rotation period for the maritime pine in the study area. The longer term (2 year) impact of PPM defoliation on tree growth were examined in a subset of seven stands aged from 9 to 30 years old in which no subsequent defoliation (winter 2010–2011) were observed.

Trees were allocated in one of five defoliation intensity classes (% of defoliated crown): 0%, (control) 25%, 50%, 75%, and 100%. Percent defoliation was visually assessed to the nearest 5% by two ground-based observers, using binoculars whenever necessary. Old foliage contributes ca. 50% of tree crown area in maritime pine (Porté et al., 2000). Furthermore, PPM caterpillars prefer to feed on older needles and shift to current year needles when the former are entirely consumed. Trees were considered to be 25% defoliated if half of the mature needles were missing. Trees were considered to be 50% defoliated if all of mature needles were missing. Trees were considered to be 75% defoliated if all of the mature needles and half of the current year needles were missing and 100% if all mature and current year needles were missing. All classes of defoliation were represented within each of the 11 sampled stands. A stratified tree sampling design was applied, with the defoliation intensity factor nested within the stand age factor. For each stand and each class of defoliation intensity, we sampled three trees of same status, for a total of 165 sampled trees (15 per stand).

2.3. Artificial defoliation experiment

To investigate whether artificial defoliation had similar growth impacts to natural defoliation, needles were snipped manually with scissors 0.5 cm from the brachyblast to mimic PPM feeding. The artificial defoliation was carried out in February 2010 and coincided with the end of natural PPM feeding period. Removed needle material was left at the tree base. The same five classes of defoliation intensity as assessed in natural defoliation experiment were replicated in this trial. Artificial defoliation was applied to trees belonging to the stands where the effect of natural defoliation was assessed, allowing true paired comparisons. Because older stands were too high (more than 10 m), canopy access was too difficult, it was thus impossible to defoliate trees older than 10 years old. So for this study, only the four youngest stands (3, 6, 9, and 10 years old) were used. Within each stand two trees

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