



Effect of host tree density and apparency on the probability of attack by the pine processionary moth



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ABSTRACT

The pine processionary moth (PPM, *Thaumetopoea pityocampa*) is the main defoliator of pines in the Mediterranean area, necessitating constant surveillance and regular pest management. A sound understanding of the spatial distribution of infested trees, both within and between stands, is required to increase management efficiency. We hypothesized that both host tree density at stand scale and tree apparency at individual tree scale were responsible for between- and within-stand patterns of PPM infestation. We tested these hypotheses on a sample of 171 maritime pine stands in the Landes de Gascogne, the largest plantation forest in Europe. We showed that PPM infestation (percentage of infested trees) decreased significantly with stand density, and was therefore greater in older than in younger stands. The probability of a pine tree being attacked increased significantly with tree height and proximity to the edge of the stand. Mortality rates of exposed sentinel egg batches did not differ with distance from the stand edge. We discuss three likely explanations for higher infestation of taller trees at stand edges: better survival of larvae on sun-exposed trees, and random interception vs. active host selection by gravid females. Our findings suggest that stand management could be adapted in order to decrease the risk of damage by the pine processionary moth, and that predictive tools for infestation dynamics can be based on forest growth models.

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1. Introduction

The pine processionary moth *Thaumetopoea pityocampa* [Denis and Schiffermüller] (Lepidoptera, Notodontidae) hereafter referred to as PPM, is, by far, the most important forest pine defoliator in Southern Europe and North Africa, in terms of its temporal occurrence, geographic range and socioeconomic impact. PPM causes periodic outbreaks, with high rates of defoliation, at intervals of two to ten years (Robinet, 2006; Hódar et al., 2012). It is found in all the countries of the Western Mediterranean (Huchon and Démolin, 1971) and is currently spreading to higher latitudes, probably in response to climate change, with increasing winter temperatures (Battisti et al., 2005; Robinet and Roques, 2010). PPM larvae feed on pine needles during the fall and winter. This significantly decreases tree growth on the short-term (1–2 years

after defoliation), even at low levels of defoliation (Jacquet et al., 2012, 2013). However, trees seem able to recover on the long-term if defoliation is not so frequent (Linares et al., 2014). In addition to this effect on forest health, PPM caterpillars have urticating hairs, and may therefore cause health problems for people living in newly colonized urban areas (Battisti et al., 2011). Monitoring and pest management actions are therefore required on a regular basis, to ensure the detection, evaluation and mitigation of potential risks to forest and public health (Jactel et al., 2006; Cayuela et al., 2011). However, we still lack some of the basic knowledge required for relevant analyses of the risk posed by PPM. In particular, the mechanisms controlling the distribution of PPM attacks within and between pine stands remain unknown.

Pest risk is defined as a combination of three components: (1) hazard occurrence, which depends on the spatiotemporal dynamics of pest populations; (2) plant vulnerability to hazard, resulting in a certain amount of damage; and (3) the economic impact of damage, depending on the potential value of the plants damaged (Jactel et al., 2012). For the determination of each of these components,

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we need to know which trees are likely to be attacked by PPM. Conventional population monitoring is based on counts of winter nests built by late-instar larvae of PPM and visible in tree crowns (Geri and Miller, 1985; Jactel et al., 2006). This sampling method could be improved by better knowledge of the spatial distribution of attacked trees, both between and within pine stands. It has recently been shown that the frequency of infestation with PPM is higher for trees at the stand edge than for trees at the heart of the stand (Dulaurent et al., 2012), but it remains unclear whether the infested trees are randomly distributed or aggregated within stands (Arnaldo and Torres, 2005).

Feeny (1970) coined the term “plant apparency” to describe the likelihood of a plant being identified by its herbivore enemies. This original definition has been extended to include two key features underlying plant apparency (Castagneyrol et al., 2013): the individual size, color or odor of the plant, and its relative abundance within the plant community. At the stand scale, the probability of an individual tree being attacked by PPM would be expected to decrease with increasing tree numbers, i.e. in denser stands, due to a dilution process, as reported by Geri and Miller (1985). At the individual tree scale, the probability of attack is generally dependent on the insect’s perception of the physical or chemical cues provided by the host tree. Insect herbivores may locate host trees through visual cues (Prokopy and Owens, 1983), such as tree color (Goyer et al., 2004; Campbell and Borden, 2009) or shape. For example, Dulaurent et al. (2012) showed that the planting broad-leaved hedgerows next to pine stands reduced the number of attacks on the pines growing behind the hedgerow. The magnitude of this effect was dependent on the relative heights of the pines and the broadleaved hedge trees. It was strongest for pines surrounded by taller broadleaved trees, suggesting that pine height may be a critical factor determining the likelihood of attack. Similarly, Floater and Zalucki (2000) found that taller trees were more easily located by the processionary caterpillar *Ochrogaster lunifer*. Plant odors also play an important role in host recognition and location by insects (Visser, 1986; Bruce et al., 2005; Tasin et al., 2006), but are more likely to be used over long distances, for the identification of suitable habitats (Zhang and Schlyter, 2003), or to distinguish between host and non-host plants in mixed patches of vegetation with high levels of diversity. The presence of non-host trees, such as birch, has been shown to disrupt pine recognition by PPM, due to the release of non-host volatile compounds (Jactel et al., 2011).

We hypothesize that the probability of a tree being attacked, for a given local PPM density, depends primarily on two key features related to different spatial scales: (H1) host density at the stand scale, with a higher probability of attack in older stands in which tree density is lower, and (H2) tree proximity to edge and host apparency, where proximity to edge might reflect either random choice from imago emerging from the soil outside pine stands (H2.1), a better survival of eggs and larvae at the edges because of higher temperatures (H2.2), or active PPM female choice for more apparent trees (H2.3). We tested these hypotheses by determining the percentage and distribution of the trees attacked by PPM in 145 stands of the largest pine plantation in Europe during a period between outbreaks. To investigate the mechanisms underlying PPM winter nests distribution, we experimentally tested whether the mortality rate of PPM egg batches differed according to their location within pine stands.

2. Materials and methods

The study was carried out in the Landes de Gascogne forest, in South West France. This region is dominated by 800,000 hectares of single species plantations of maritime pine (*Pinus pinaster*), of

similar age. We used and re-analyzed two datasets described in detail by Samalens (2009) and Castagneyrol et al. (2014), an overview of which are provided below. The first dataset was used to study the effects of host density (H1), tree distance to stand edge and host apparency (H2.1 vs. H2.3) on PPM infestation, whereas the second dataset was used to test the effect of temperature on egg survival (H2.2).

2.1. Datasets

2.1.1. Dataset 1

Data for PPM infestations were collected in 2005 from 145 pure stands of maritime pine (*P. pinaster*) sampled along a systematic grid of 2 km near Pontenx-Les-Forges (44°14'N, 00°07'W) and covering a 16 × 16 km area (i.e. 25,000 ha) in the heart of the Forêt des Landes de Gascogne (Fig. 1A).

The aspect (i.e. North [N], North-East [NE], East [E], South-East [SE], South [S], South-West [SW], West [W], or North-West [NW]) of the sampled edge was recorded. Stands were between four and 61 years old and their density ranged from 113 to 2500 trees/ha. Individual trees were between 2 and 28 m in height and 3.9 and 49.2 cm in diameter.

Within each of the stands sampled, four sampling plots were set up: an “edge plot” (EP) of 20 neighboring trees was established along the stand edge and three “interior plots” (IP1, IP2, IP3) of 20 neighboring trees were established within the heart of the stand, 25 m apart, in a cross-shaped design (Fig. 1B). Tree density decreased with increasing stand age. When stand density was very low (e.g. in 7 old stands) only 10 trees per plot were sampled to make sure that sampled plots were small enough to be homogeneous in terms of site conditions. In spring 2005, tree height was measured for a subsample of 29 trees per stand, corresponding to all 20 trees from one of the inner plots plus the three largest trees of the other three plots. Diameter at breast height was recorded for all trees of each plot. PPM population density (number of nests/ha) was calculated from the number of nests per sampled tree, the number of trees sampled, tree density and the area of the sampled plots. In total, 11,353 pine trees were included in this analysis (see Samalens, 2009 for further details).

2.1.2. Dataset 2

Egg batches were obtained from a laboratory rearing program in spring 2011. Details of the method used have been reported elsewhere (Castagneyrol et al., 2014). Fifty egg batches were distributed between five pine stands, in which two trees were selected at random at each of five different distances from the stand edges (0, 2, 6, 8 and 16 m). A single egg batch was attached to each tree, on a branch at the base of the tree crown. Sentinel egg batches were protected against predators and parasitoids with a fine mesh (0.05 × 0.05 cm), to ensure that any deaths were due to abiotic factors only. One of the two egg batches exposed at each distance from the edge was associated with a Hobo® data logger (Fig. 2). Temperatures were recorded at 30-min intervals, from the start of the experiment until the end of the egg hatching period (i.e. 50 days later). The egg batches were removed at the end of August and egg mortality was determined, as a percentage, in the laboratory (see Castagneyrol et al., 2014). The data for this experiment were recorded as dataset 2.

2.2. Statistical analyses

Analyses were carried at both the plot and tree scales. The number of nests per hectare, stem density and aspect were determined at stand scale. These variables were therefore included in models with stands as replicates. Tree height and diameter, and the presence/absence of nests on sampled trees were tree-specific

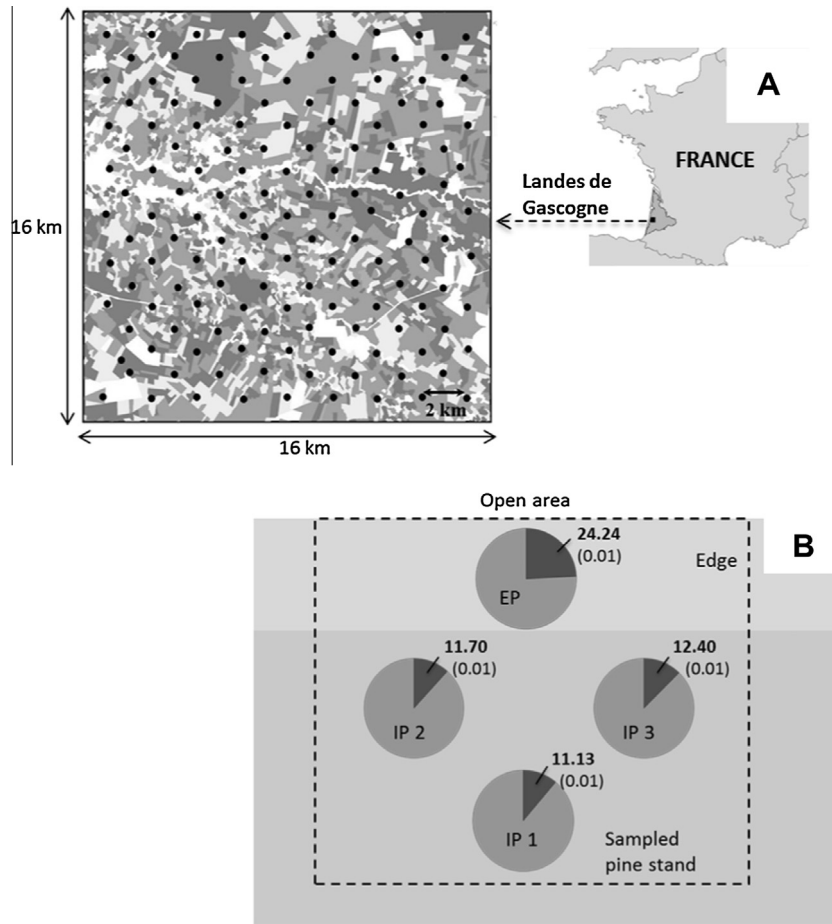


Fig. 1. Sampling design corresponding to dataset 1. (A) Location of sampled maritime pine stands. Sampled stands were located along a grid of 2×2 km. Gray colors are maritime pine stands of various ages and white color is open and broadleaf areas (Source: Samalens, 2009—Figure published with author's agreement). (B) Location of experimental plots within sampled pine stands. Values in bold characters represent the actual percentage of attacks (\pm SE) averaged across the 145 stands. The pie charts represent edge (EP) and inner plots (IP). The dark slices represent the percentage of trees infested.

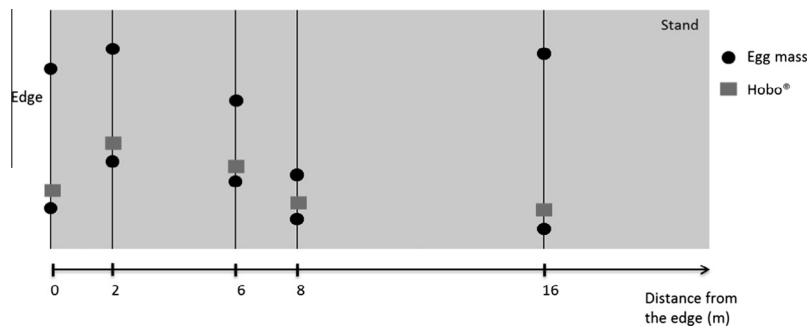


Fig. 2. Location of sentinel egg batches in maritime pine stands corresponding to dataset 2. Please note that within a given distance to the edge, distance between trees on which egg batches were install was presented arbitrarily and may have differed among stands.

attributes and were analyzed in models with trees as replicates. All statistical analyses were performed with R software (R Core Team, 2012).

2.2.1. Effects of stand attributes on PPM infestation (dataset 1)

Generalized linear models were used to assess the effect of stand characteristics on PPM infestation in the 145 independent sampled stands. All stand characteristics (age, stem density, mean tree diameter and height) were strongly correlated (all pairwise correlations with $|r| > 0.84$ and $P < 0.001$). The older stands were also less dense, with larger and taller trees. These correlations

prevented the simultaneous use of these variables in the same model (Graham, 2003). We used stem density as an explanatory variable in linear models, rather than stand age, mean tree height or diameter, as stem density is easier to estimate and to control through forest management (e.g. by thinning).

We first assessed the effect of stem density on the mean number of nests per hectare (PPM population density) using a GLM with a Poisson error distribution accounting for overdispersion ["dispmod" R package (Scrucca, 2012); see also Breslow (1984)]. GLM with binomial error were used to assess the effect of stem density on the percentage of infested trees (Williams, 1982).

2.2.2. Effects of tree attributes on the probability of a tree being attacked by PPM (dataset 1)

The same dataset was used to test the effects of tree attributes (height, diameter and location within stands) on the probability of a tree being attacked by PPM, but with trees as replicates. The individual trees could not be considered to be independent, due to the sampling design (trees nested within plots, nested within stands) and therefore mixed-effect models were used, with stands and plots treated as nested random factors. Tree diameter was positively and strongly correlated with tree height ($n = 3334$, $r = 0.905$, $P < 0.0001$), precluding the inclusion of these two variables together in the same model (Graham, 2003). Tree height is harder to measure reliably (particularly as trees grow taller) and tree diameter was measured on all trees. We therefore preferred to use tree diameter in our analyses. Although tree diameter and stand density were not independent (because of regular thinning as trees grow larger), both variables are likely to control tree infestation by the PPM, and it is important to tease apart these two potential effects. We therefore built first a binomial (GLMM) to analyze the presence/absence of PPM nests on individual trees, using the following fixed effects: stand density + tree diameter + plot location + tree diameter \times plot location. The interior plots (IP1, IP2 and IP3) were pooled together so that plot location was treated as a two-level factor, contrasting edge plots vs. interior plots. This first model was then simplified by sequentially removing explanatory variables, starting by the two-ways interaction. This set of models was compared using information theory. The set of best-fitting models was selected based on Akaike's information criterion, corrected for small sample sizes (AICc, Burnham and Anderson, 2002) using the selMod function from the "pgirmess" package (Giraudoux, 2013). Among the best fitting models, the minimum adequate model (MAM), i.e. most parsimonious model, was that with the lowest number of estimable parameters (K) within 2 AICc units of the model with the lowest AICc. Differences in AICc scores (Δ_i) of >2 are usually interpreted as indicating strong support for the MAM compared to poorer models (Burnham and Anderson, 2002). For each explanatory variable, Akaike's weights were summed across all models in which it occurred, in order to quantify their relative importance (w_H , the larger the sum, the more important the variable relative to the other variables used in same candidate models, Burnham and Anderson, 2002). Maximum likelihood approximation instead of restricted maximum likelihood approximation was used to estimate model parameters. Model R^2 values were calculated as described by Nakagawa and Schielzeth (2013). GLMMs were fitted with the lmer function of the "lme4" R package (Bates et al., 2013).

2.2.3. Edge effect on the rate of infestation by PPM (dataset 1)

We explored the edge effect further, by splitting dataset 1 and using only edge plots (EP) to test the effect of edge aspect on the rate of infestation by PPM. We investigated whether the percentage of infested trees along edges differed between edge aspects, using the tree function of the tree package in R (Ripley, 2013). This function "grows" a tree by binary recursive partitioning and establishes nodes separating predetermined factors (here the eight aspects) on the basis of their attributes (here the percentage of infested trees). This procedure makes it possible to group together the aspects most similar in terms of PPM infestation.

2.2.4. Effect of distance from stand edge on PPM egg mortality (dataset 2)

To assess the effect of distance from stand edge on egg mortality in sentinel batches, we analyze the effects of edge distance on the percentage of hatched eggs, using a binomial response variable (number of hatched eggs vs. number of non-hatched eggs), with GLMM. We accounted for spatial pseudoreplication (i.e. 2 egg batches at each distance from stand edge), by nesting distance to

the edge within the random site effect. The same approach as described above was applied to select the best model and estimate model parameters. Likewise, we assessed the effect of distance from stand edge on mean daily temperature and the number of days to reach the cumulative mean temperature of 780 °C proposed by Démolin (1987) to be required for completion of the egg stage (from oviposition to hatching).

3. Results

3.1. Effects of stand attributes on PPM infestation (dataset 1)

On average, $14.86 \pm 0.33\%$ (mean \pm SE) trees per stand were attacked by PPM, in the 145 stands sampled in 2005 (dataset 1). The mean number of nests per infested tree was 1.36 ± 0.02 , indicating a moderate level of infestation (endemic conditions).

PPM population density (i.e. number of nests per ha) was not related to stand density ($P = 0.50$, $\chi^2 = 0.394$), whereas the rate of infestation by PPM (i.e. the percentage of attacked trees) decreased significantly with increasing tree density ($P < 0.0001$, $\chi^2 = 61.519$, Fig. 3).

The number of infested trees was therefore greater in older stands, which contained fewer trees.

3.2. Effects of tree attributes on the probability of a tree being attacked by PPM (dataset 1)

The contributions of stand density, tree diameter and tree location to the probability of PPM attack were strongly supported by model selection since the two best models included these three variables as predictors (Table 1). Trees were more likely to be attacked in edge plots than in inner plots (IP, Figs. 1 and 4). The probability of individual tree being attacked also increased with tree diameter (Fig. 4). Because of the strong correlation between pine height and diameter, this implies that taller trees were more likely to be attacked than smaller ones. The model including the diameter \times location interaction was within a $\Delta\text{AICc} = 2$ units of the best model, but the weight of this interaction was weak ($w_H = 0.31$, Table 1) as compared to the weights of diameter ($w_H = 1$), location ($w_H = 1$) and density ($w_H = 0.82$). The comparison of marginal ($R_m^2 = 0.41$) and conditional ($R_c^2 = 0.18$) R^2 indicates that more variance (23%, $R_m^2 - R_c^2$) in probability of attack was explained by the random effects (i.e. stand and plot) than by fixed effects (18%).

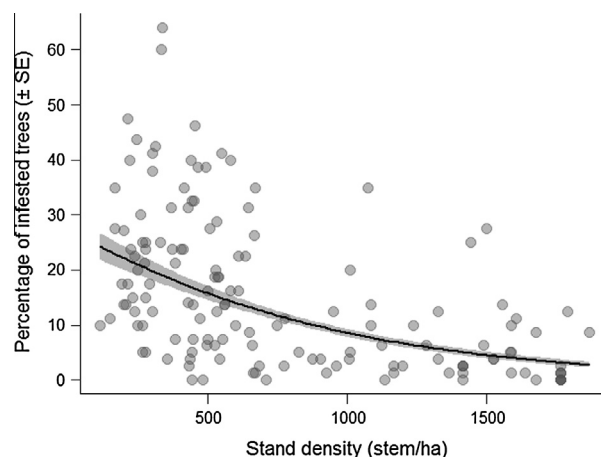


Fig. 3. Effect of stem density on the percentage of pines infested by PPM per stand. Each dot represents an individual stand. The solid line and shaded area represent the prediction of the model and the corresponding standard error.

Table 1

Summary of model selection testing the effect of tree diameter and location within stand on the probability of attack by the pine processionary moth. Model parameter estimates that are given correspond to estimates of the best model. Density: stand density; diameter: individual tree diameter at DBH; location: plot location within stand (edge vs. interior).

| Fixed effects | AICc | Δ AICc | w_{ic} |
|--|---------|---------------|----------|
| Density + diameter + location | 7882.00 | 0.00 | 0.51 |
| Density + diameter + location + diameter \times location | 7883.02 | 1.01 | 0.31 |
| Diameter + location | 7884.04 | 2.03 | 0.18 |
| Density + diameter | 7999.53 | 117.53 | 0.00 |
| Diameter | 8000.51 | 118.50 | 0.00 |
| Density + location | 8006.16 | 124.16 | 0.00 |
| Location | 8068.95 | 186.95 | 0.00 |
| Density | 8136.61 | 254.60 | 0.00 |
| Null | 8200.35 | 318.35 | 0.00 |

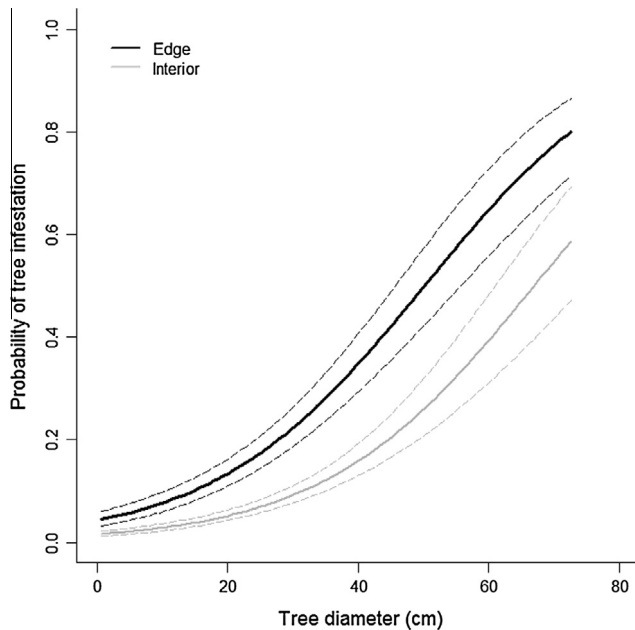


Fig. 4. Effect of tree diameter and location within stands on the probability of attack by the pine processionary moth. Solid and dashed curves indicate the model predictions and the corresponding SE, respectively.

3.3. Effect of edge aspect on the rate of PPM infestation (dataset 1)

Binary recursive partitioning identified two nodes, splitting the dataset into three groups of edge aspects on the basis of PPM infestation rate. The first node separated edges with westerly and south-westerly aspects from all other edges. Infestations levels were highest in this group, with, on average, 34.8% trees attacked by PPM (Fig. 5). The second node split the remaining edges into two groups: moderately infested edges (South, South-East, East and North-West, Fig. 5) with, on average, 24.7% of trees attacked, and edges with low levels of PPM infestation (North, North-East, Fig. 5), with a mean of 19.1% of trees infected.

3.4. Edge effect on PPM egg mortality (dataset 2)

Distance from stand edge did not contribute to the explanation of egg mortality in sentinel egg batches as model including this predictor (AICc = 1598.77) was within 2 units (Δ AICc = 0.98) of the null model (AICc = 1597.79), suggesting that pattern of nests aggregation at stand edge was not due to lower egg mortality at this location.

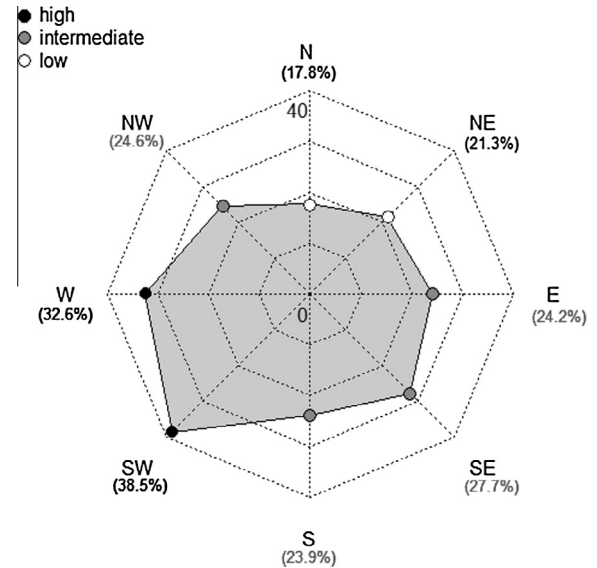


Fig. 5. Mean percentage of PPM-infested trees in stand edges, as a function of their aspect. Dot colors correspond to the three classes of PPM infestation as revealed by the classification tree (high: black, moderate: gray and low: white).

The mean daily temperature did not differ depending on distance from stand edge as model including it (AICc = −45.77) was within 2 units (Δ AICc = 1.61) of the null model (AICc = −47.37).

The cumulative mean daily temperatures of 780 °C required for hatching was reached between 40 and 42 days after exposure of the egg batches, regardless of distance from stand edge.

4. Discussion

These findings clearly demonstrate that PPM nests and PPM-infested trees are not evenly distributed within and between pine stands.

We initially hypothesized that the probability of a tree being attacked by PPM was dependent on stand characteristics, such as tree density (H1). We found that PPM population density (number of nests/ha) did not differ significantly between stands and was not correlated with stand density. This finding questions the host concentration hypothesis, according to which insect load should be greater in stands containing a larger number of host trees (Root, 1973). By contrast, it is consistent with the long-range dispersal capacities (several km) of the PPM (Robinet et al., 2012) and with the observation of spatial autocorrelations of PPM densities of the order of several kilometers (Samalens and Rossi, 2011). In our study area, maritime pine plantations account for more than 90% of the land cover (Samalens, 2009). Moreover, PPM data were collected in 2005, during a latent phase between two outbreaks, when the abundance of this pest was moderate (Pauly, 2007). It is therefore probable that feeding resources (maritime pine trees) were abundant enough with respect to the PPM population, ensuring that female moths were able to find suitable habitats throughout the landscape, thus yielding a uniform distribution of nests across pine stands.

By contrast, rates of infestation with PPM were dependent on stand characteristics. The percentage of trees attacked by PPM was higher in older stands, which had a lower tree density. For a given load of moths potentially able to attack trees, which was equal across stands, the probability of a tree being attacked in pure maritime stands was thus higher at lower host densities. Geri and Miller (1985) observed a similar pattern of infestation, with a larger number of infested trees in less dense pine stands. Negative

correlations between tree density and percentage of tree infestation with herbivorous insects are commonly reported for other conifer defoliators, such as the pine sawflies *Neodiprion autumnalis* in the US (McMillin et al., 1996), *Diprion pini* on Scots pine in Finland (De Somviele et al., 2004), and *Neodiprion abietis* on balsam fir in Canada (Ostaf et al., 2006). These patterns of infestation may be explained by low pest density (endemic populations), unlimited feeding resources, and non-random host colonization processes leading to the infestation of a constant number of more suitable trees (De Somviele et al., 2004).

We observed that trees located at the edge of stand were more likely to be infested than trees located in the heart of stand. Higher rates of infestation at forest edges have already been reported for the pine processionary moth in the study area (Dulaurent et al., 2012), and in mountainous areas (Geri and Miller, 1985; Barbaro et al., 2013). Similar observations have been reported for several other forest insects (Dulaurent et al., 2012 and references therein), such as the gypsy moth *Lymantria dispar* in Mongolia (Hauck et al., 2008; Dulamsuren et al., 2010) and the bark beetle *Ips typographus* in Germany (Kautz et al., 2013).

Edges with different aspects had different rates of PPM infestation. Attacks were concentrated on edges facing west and south-west, corresponding to the edges receiving the most sunlight in this area. Conversely, shadier edges (North and North-East) had the lowest rates of PPM infestation, whereas edges facing south-east and north-west had intermediate levels of infestation. This trend is consistent with previous observations in mountainous areas (Barbaro et al., 2013).

Regardless of the location of trees within stand, their probability of being attacked by PPM increased with tree diameter. Given the strong correlation between tree diameter and height, this result also implies that taller trees were more likely to be attacked than shorter ones.

The uneven distribution of PPM nests within the stands, e.g. on higher trees and trees located at stand edges may be explained by three main non-exclusive hypotheses. The first one (H2.1) is that PPM female moths are rather unselective when ovipositioning as suggested by Hódar et al. (2002). As imagoes usually emerge from the soil outside pine stands, female pine processionary moths would just by chance first encounter edge trees or be intercepted by trees with larger crown. According to this hypothesis, the within stand distribution of PPM nests may simply result from passive interception of gravid females by particular trees. Alternatively (H2.2), a better survival of eggs and larvae on taller trees or on trees located at stand edges may be expected because they would benefit from more sunshine and then higher temperatures in winter, thus leading to better conditions for development (Battisti et al., 2013). The last hypothesis (H2.3) is that the probability of an individual tree being attacked by the PPM would result from an active PPM female choice for more apparent trees, either due to their location at stand edge (Dulaurent et al., 2012) or their higher height.

The edge effect on PPM infestation can account to both “random interception” and “active host selection” hypotheses (H2.1) and (H2.3). Pérez-Contreras and Tierno de Figueroa (1997) showed that the number of PPM egg batches increased with pine height and was significantly different between the two pine species (*Pinus halepensis* and *P. pinaster*) in mixture. More recently Pérez-Contreras et al. (2014) showed again that, independently of the pupation site, gravid females of pine processionary moth were able to choose for ovipositioning between two host pine species (*P. halepensis* and *P. pinaster*), even if these pine species were randomly distributed within a stand. Although these findings indicate that females can discriminate and actively select their host between two pine species, they do not bring information on female selection amongst individual pines of the same species. Therefore,

despite a partial support for H2.3 (i.e. active host selection), the alternative hypothesis (random interception H2.1) cannot be fully discarded. Further experiment should focus on female flight behavior during the oviposition period in order to arbitrate between these two hypotheses (H2.1 vs. H2.3).

The main reason put forward for the lower mortality of PPM on taller trees and/or trees located at the stand edge (H2.2) is that they receive more sunshine, resulting in a more favorable microclimate for the offspring (Battisti et al., 2005, 2013; Buffo et al., 2007). PPM larvae are thought to prefer spinning their nests on parts of the tree crown exposed to sunshine, where they can absorb warmth and are likely to be more resistant to low winter temperatures (Geri, 1980, 1984; Hoch et al., 2009). In our experiment, we found no significant difference in egg survival, in relation to distance from stand edge. We also showed that there was no difference in mean daily temperature between trees at different distances from the stand edge. Our finding show that PPM nests were more abundant in South-West facing edges yet the “better survival” hypothesis (H2.2) cannot be discarded. Our experiment was conducted in summer, when temperatures are not limiting, and then does not provide information about larvae survival during the winter. Further research would be needed to compare winter temperatures in larval nests located on sun exposed vs. shaded branches.

Whether the concentration of PPM attacks on taller trees and at the edge of the stand reflects the active selection of host trees by females rather than differences in offspring's mortality is consistent with the observation that female pine moths use the silhouette of a tree visible against a light background as a visual clue for the selection of host trees (Démolin, 1969). Following pupation in the soil of open habitats adjacent to woodland (Dulaurent et al., 2012), adult female PPMs emerge at dusk, mate and start laying eggs before nightfall of the same day (Démolin, 1969). The trees most visible from the pupation areas would therefore be those at stand edges and taller trees, which would have a crown silhouette more clearly distinguishable against a clear background than smaller trees, which would be hidden by their taller neighbors. Greater rates of infestation for the sunniest edges (facing West) may be also explained by a greater lightning of these edges at dusk, facilitating the orientation of flying females prior oviposition.

5. Conclusion

This study provides new evidence supporting the hypothesis that pine processionary moth attacks on individual trees result from mechanisms acting at two different scales. At the stand scale, there was a negative relationship between the percentage of infested trees and stem density, but no relationship was found between stem density and PPM winter nest density. At the tree scale, the probability of individual trees being infested is greater for trees located at the stand edge and for larger trees. However the mechanisms that trigger such infestation pattern could not be fully disentangled. In particular further research is needed to explore the possible active host selection vs. random interception processes by female moths.

These new findings will help to improve the monitoring of PPM at a time at which this species is spreading to new forest areas in response to global warming (Robinet, 2006). For example, our findings suggest that early warning detection systems should focus on stand edges, supporting the use of roadside sampling methods to cover large areas in a cost-effective approach (Samalens et al., 2007). Our results also pave the way for improvements in PPM risk analysis models. They clearly show that stand vulnerability can be predicted from a combination of information about the location of the tree within the stand and the frequency distribution of tree heights (or diameters): two basic outcomes of forest growth models.

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