Forest Ecology and Management 389 (2017) 136–148

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Modelling spatiotemporal dynamics of *Pinus pinea* cone infestation by *Dioryctria mendacella*

Rafael Calama [a,c,*], Mathieu Fortin [b], Marta Pardos [a,c], Rubén Manso [b]

[a] INIA-CIFOR, Ctra A Coruña km 7.5, 28040 Madrid, Spain
[b] INRA/AgroParisTech, UMR 1092 LERFoB, 54000 Nancy, France
[c] iuFOR INIA-UVa, Spain

ARTICLE INFO

Article history:
Received 7 September 2016
Received in revised form 15 December 2016
Accepted 16 December 2016
Available online 6 January 2017

Keywords:
Forest pest
Seed predation
Mediterranean stone pine
Binomial mixed model
Spatiotemporal correlation
Masting

ABSTRACT

Insect predation on seeds of forests species during the predispersal phase is a special case of plant-pest interaction in which, while plant survival and growth is not threatened, natural regeneration can be negatively affected. In the case of seeds with a high economic value, as is the case of nuts from the Mediterranean stone pine (*Pinus pinea* L.), predispersal predation can also result in severe economic losses. The insect-seed relationship shows complex spatiotemporal dynamics, including patterns of dependency between fruit availability and fluctuations in insect population, occurrence of insect outbreaks, spatial contagion and masting habit.

In the present study, we focus on the damage caused by a native pest, the *Dioryctria mendacella* Stgr. moth, to cones and seeds of *P. pinea*, a forest species showing a marked masting habit. We firstly identified those environmental and stand-level factors controlling the spatiotemporal pattern of damage by *D. mendacella*, as well as the self-regulatory effect that interannual variability in seed production could have on the population dynamics of the moth. In a second phase, we constructed a predictive phenomenological model to forecast the probability of cone damage in a given location, as well as the expected patterns of spatiotemporal spread and dispersion.

Our results revealed a strong correlation between the probability of damage and crop size in a given year, pointing to a dependency between feeding resources and predator population. Additionally, the probability of damage is affected by the number of damaged cones observed in the previous year, indicating temporal contagion. Cone and seed damage is also affected by the temperature during different phases of the complex life-cycle of *D. mendacella*, which suggests that breakout processes are synchronized within the territory and linked to the occurrence of bumper crops and favorable climatic conditions. We detected that the level of infestation at a given location is related to site and environmental conditions, with no significant pattern of contagion/spreading from stands with high resource availability to those with low availability. Damage prediction under warmer climate scenarios reveals a counterbalance among favorable/unfavorable conditions for insect expansion and expected decline in cone production, resulting in only slight changes.

1. Introduction

Native forest insects pests, although integral components of forest ecosystems, have considerable influence on the health, structure and functionality of forests (FAO, 2009). They can adversely affect tree growth, vigor and survival, as well as functional processes such as nutrient cycling, photosynthesis and the ecological succession of the forest (McCullough et al., 1998). From an anthropocentric point of view, forest pests influence the yield and quality of wood and non-wood products, as well as other ecosystem services such as wildlife habitats, recreation, aesthetics and cultural values, resulting in severe economic losses and social detriment (Holmes, 1991; Robinet et al., 2013). Early, localized prediction of the abundance, potential damage and expected outbreaks of a given native forest pest is a basic demand from managers, owners, industry and policy makers (Plant and Mangel, 1987). Prompt knowledge of the expected temporal and spatial dynamics of insect damage is essential for prioritizing areas with regard to adopting appropriate management tactics, defining techniques for pest

* Corresponding author at: INIA-CIFOR, Ctra A Coruña km 7.5, 28040 Madrid, Spain.
E-mail address: rcalama@inia.es (R. Calama).

http://dx.doi.org/10.1016/j.foreco.2016.12.015
0378-1127/

control, providing insight into expected economic losses and ensuring raw material supply for industry.

The spatiotemporal distribution of forest insect pests is influenced by many intrinsic and extrinsic factors, such as the presence of predators, feeding resource availability, habitat heterogeneity, climate, and dispersal capacity (Aukema et al., 2008). Understanding the spatial and temporal dynamics of pest species and the factors involved is basic in any attempt to forecast the degree of infestation, the occurrence of insect breakout or their spread to new areas (Gumpertz et al., 2000; Sakai et al., 2001). Under future changing climate scenarios, forecasting increases in temperature, range distribution, abundance and severity of damage caused by native forest pests is expected to change (Pinkard et al., 2010; Chen et al., 2011; Wainhouse et al., 2014). Thus, long term forest management planning should take into account the potential effect of these changing scenarios on pest dynamics and would require reliable tools to predict the impact of forest pests (Gumpertz et al., 2000).

Insect predation on seeds during the predispersal phase is a special case of plant – pest interaction (Sallabanks and Courtneys, 1992), in which the feeding resource is not the plant-itself, but some of its reproductive bodies, such as fruits or seeds. While processes of plant population dynamics such as seed dispersal, subsequent plant regeneration and long term persistence of the forest can be influenced by seed predation, mother tree survival and vigor is not affected (Kulkarni and Joshi, 1998). Additionally, the predator satiation theory (Kelly, 1994) postulates that the masting strategy observed in many species results in alternating periods of satiation-starvation for seed predators. Finally, seed production is a highly spatially-explicit attribute, showing spatial heterogeneity at different scales (Calama et al., 2008). Thus the mechanisms of pest dynamics, population fluctuations and spreading patterns in seed–insect relationships can be considered a complex spatio-temporal process involving dependencies across a wide range of spatial and temporal scales (Turgeon et al., 1994).

Significant patterns of spatial correlation in the intensity of seed predation would indicate a pattern of dependency between insect population, seed production and spatial attributes (Preisler et al., 1997), such as orography, soil, stand maturity, average climate, and historical forest management practices. Additionally, temporal dependencies among the levels of infestation could be due to (i) climate-driven masting in seed production, (ii) predator-prey processes, where the number of predators fluctuates with the availability of the resource (seed) in the current and previous years or (iii) a delayed regulation of the insect population due to the effect of parasitoids. Finally, the identification of a pattern of spatiotemporal correlation would provide insight into the pattern of contagion, allowing the prediction of future spread and expansion of the pest within the territory (Aukema et al., 2008).

Pine nuts from stone pine (*P. pinea* L.) are one of the most important non-wood forest products in Mediterranean forests. Ripe, healthy cones are collected annually from standing trees, resulting in larger incomes for forest owners than those derived from timber harvesting (Mutke et al., 2012). The cones collected are then industrially processed in order to extract the unshelled white nuts, the valuable end product, with current prices over 100 €/kg. *P. pinea* shows a strong masting habit, resulting in interannual differences in cone production within the same region of 20-fold between bumper and non-productive years (Mutke et al., 2005). Masting in the species is largely controlled by climatic factors, particularly by rainfall events during the processes of bud formation and floral induction. However, a resource depletion process resulting in an inhibition of female floral production the year after a bumper crop was also identified (Calama et al., 2011). This finding indicates that masting in the species is not a mere resource matching process, but an evolved reproductive strategy which is in agreement with the predator-satiation theory (Kelly and Sork, 2002).

Two native insects are the main agents of biotic damage in immature cones of *P. Pinea* throughout the area of distribution of the species: the pine cone moth *Dioryctria mendacella* Stgr. (Lepidotera: Pyralidae) and the weevil *Pissodes validirostris* Gyll. (Coleoptera; Curculionidae). The process of flowering and cone ripening in *P. pinea* lasts three years (Mutke et al., 2012), and larvae of both species feed within the cones during the last year of maturation. The cones attacked by the pine cone moth commonly maintain their size, but damage is easily identifiable since they bear resin exudates, browning of the damaged bracts, partial abortion of the cones and severe damage to pine nuts (see Fig. S1). In contrast, cones damaged by the weevil usually interrupt their growth before complete maturation, bearing a pale brown color over the surface, not showing resin exudates and exhibiting perfectly circular-shaped apertures used by the adult insect (Romanyk and Cadahia, 1992). In any case, damaged cones often lose all their commercial value. While *Pissodes validirostris* was traditionally considered the most important pest affecting cones in the inner regions of Spain (Baudin, 1967), recent studies (Ferrera, 1991; Junta de Castilla y León, 2014; Pajares, 2016) have pointed to a major incidence of *D. mendacella.* Although not exhaustively studied, the current level of damage caused by *D. mendacella* can reach 20–30% of the total annual cone production, with areas where damage can be up to 80–90% (Baudin, 1967; Ferrera, 1991).

D. mendacella has a complex and little-understood life cycle (Romanyk and Cadahia, 1992), with a minimum of two adult generations per year. The flight of the different generations of adult moths and the infestation of cones can occur from mid-spring to the beginning of fall (Pajares, 2016), affecting cones in the last phases of maturation. As a consequence, progeny of different adult generations at different stages of development can be found in the same cone (Ferrera, 1991). This complex cycle hinders both the identification of the factors driving the population fluctuations and the elaboration of management control techniques.

In the present study, we aimed to provide an insight into the potential damage caused by *D. mendacella* to *P. pinea* cone crops within the Central Range of Spain. More specifically, we attempted to identify climatic, site and stand-related factors influencing the spatiotemporal pattern of damage by *D. mendacella*, as well as the self-regulatory effect that the masting habit could have on the population dynamics of the moth. This information will allow the construction of a predictive model to forecast the probability of cone damage as well as expected patterns of spatiotemporal spread and dispersion. Our main hypotheses are: (i) given the complex lifecycle of the insect with overlapping stages, we expect that the current level of cone damage will be associated with seasonal climate events occurring during the last year of cone maturation; (ii) given the dependence of the species on a highly fluctuating resource, we expect that – in accordance with the predator-satiation theory – current and past cone production will be among the most important traits regulating the dynamics of *D. mendacella* populations; (iii) given the native character of the insect in the territory, we expect a homogenous spatial distribution of damage, derived from the recurrent movement between patches of high and low cone production and level of infestation.

2. Material

2.1. Study area

The Mediterranean stone pine (*P. pinea* L) occupies more than 30,000 ha in the Central Range in Spain. Most forest stands in this region are growing on rocky granitic slopes that define the valleys of the Alberche and Tiétar rivers, occupying an altitudinal strip that