Forest Ecology and Management 334 (2014) 232–240

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Dynamics of spruce bark beetle infestation spots: Importance of local population size and landscape characteristics after a storm disturbance

Simon Kärvemo [a],*, Björn Rogell [b], Martin Schroeder [a]

[a] Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, 750 07 Uppsala, Sweden
[b] Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, 752 36 Uppsala, Sweden

ARTICLE INFO

Article history:
Received 3 July 2014
Received in revised form 9 September 2014
Accepted 11 September 2014

Keywords:
Host tree depletion
Insect outbreak
Ips typographus
Local population
Tree mortality
Picea abies

ABSTRACT

The European spruce bark beetle *Ips typographus* (L.) is one of the most important pests of mature Norway spruce in Europe. Outbreaks are often triggered by large-scale storm disturbances, which provide the beetles with a large surplus of suitable breeding material in the form of wind-felled spruces in storm gaps. Due to high reproductive success in storm-felled trees beetle populations may become large enough to overcome defences of living trees in the summers following a storm. From a management perspective, procedures enabling reliable predictions of local tree mortality based on the size of storm gaps would be highly valuable. Thus, in the presented study we recorded tree mortality caused by *I. typographus* during a five-year period around 35 storm gaps hosting local beetle populations, differing in size with 0–818 colonised wind-felled spruces. We then developed models to address the following questions. How does local population size in wind-felled trees influence tree mortality in the subsequent years? What other storm gap and landscape variables influence tree mortality? How does the tree mortality compare with results of earlier studies? Four gap variables and three landscape variables at four scales (500–2000 m) were included in the models. In total, 21,486 standing spruces were killed by *I. typographus* around the gaps. Tree mortality started in the second summer after the storm and peaked in the third year around most gaps. The models explained most of the variation in tree mortality around the gaps during the five-year period, accounting for 60–67% of the deviance from null models. The most important variable influencing tree mortality was the number of colonised wind-felled trees (a proxy for the size of local populations), explaining 60–64% of the null deviance. Other gap variables that significantly, and positively, affected tree mortality were the mean diameter of colonised wind-felled trees and basal area of living spruce trees in stands adjacent to the storm gaps. Of the landscape variables, the area of storm gaps in the surrounding landscape explained most of the variation in the models. The area of spruce forest also had a significant positive effect at the largest scales. The finding that the number of colonised wind-felled trees was closely related to the number of killed trees in the forest around the gaps implies that areas with numerous large storm gaps should be harvested first after large-scale storm disturbances.

1. Introduction

The European spruce bark beetle *Ips typographus* (L.) (Coleoptera, Curculionidae) is one of the most important pests of Norway spruce *Picea abies* L. (Karst.) in Europe (Christiansen and Bakke, 1988). At endemic population levels *I. typographus* reproduces in wind-felled or otherwise damaged trees while during outbreaks it kills numerous living trees. Furthermore, the magnitude of *I. typographus* outbreaks has increased in recent years (Schelhaas et al., 2003; Seidl et al., 2011) and is expected to increase further with climate changes (Jönsson et al., 2007).

The most important factor triggering outbreaks of *I. typographus* is storm disturbance (Christiansen and Bakke, 1988; Schroeder, 2001; Bouget and Duelli, 2004), which provides the beetles with a surplus of susceptible breeding material with weak defences. Hence, in this situation the densities of maternal galleries in the wind-felled trees are generally low (Komonen et al., 2011), resulting in longer galleries with more eggs, weaker intraspecific competition between the larvae, and consequently higher numbers of offspring per parent beetle (Anderbrant et al., 1985; Anderbrant, 1990). Thus, in the summers following a storm-felling the beetle populations may be sufficiently high for the beetles to overcome defences of living trees (Christiansen, 1985; Mulock and

---

* Corresponding author. Tel.: +46 18672021; fax: +46 18672890.
E-mail addresses: simon.karvemo@slu.se (S. Kärvemo), bjorn.rogell@ebc.uu.se (B. Rogell), martin.schroeder@slu.se (M. Schroeder).

http://dx.doi.org/10.1016/j.foreco.2014.09.011
0378-1127/© 2014 Elsevier B.V. All rights reserved.

Christiansen, 1986; Christiansen et al., 1987; Komonen et al., 2011). Accordingly, severe *I. typographus*-caused tree mortality generally starts in the second summer after storm disturbances (Schroeder, 2001).

During outbreaks trees killed by *I. typographus* are generally distributed in spatially well-defined infestation spots (Schroeder and Lindelöw, 2002; Kärvemo et al., 2014), as beetles are attracted by aggregation pheromones released from trees under attack, which increases the probability of colonisation of neighbouring trees. Such infestation spots may differ in size from a few killed trees to thousands of trees (Kautz et al., 2011; Kärvemo et al., 2014). Spot growth within years is caused by beetles originating from local infestation spots (i.e. re-emerging parent beetles and new generation beetles if the local population is bivoltine) and beetles immigrating from the surrounding landscape. Infestation spots may also remain to be active for several consecutive years (Schroeder and Lindelöw, 2002). This is mainly because the new generation beetles hibernate under the bark or in the litter at the base of the killed trees and consequently densities of beetles are higher in infestation spots from the previous year in the spring when the flight period starts, which increases their probability of successfully colonising standing trees nearby (Hedgren et al., 2003; Eriksson et al., 2007; Stadelmann et al., 2013). Thus, the dynamics of infestation spots depend on interactions between the local population and beetles from other sources in the surrounding landscape.

Both emigration from and immigration to an infestation spot are likely to be influenced by the size of the local population (and hence the size of infestation spots). Below a certain population threshold the local beetles may not be able to initiate successful new colonisations of standing trees after hibernation and thus all the beetles may need to emigrate (Hedgren et al., 2003; Eriksson et al., 2007). Above this threshold the proportion of emigrating beetles should decrease with increasing spot size because of the higher probability of local beetles initiating new attacks nearby, or being attracted to trees already under attack, before they have had time to disperse outside the spot (i.e. emigrate).

Because of the high dispersal capacity of *I. typographus* (Forsse and Solbreck, 1985) immigration from the surrounding landscape may strongly influence the dynamics of infestation spots. Larger quantities of pheromones are released from larger spots (with more trees under attack), which should thus attract beetles from larger distances. However, air turbulence limits the distances from which beetles can be successfully attracted to pheromone sources (Schlyter, 1992; Byers, 1999; Franklin and Grégoire, 2001; Strand et al., 2009). Numbers of immigrants may also be influenced by their flight behaviour, which has been examined in few studies, but Forsse and Solbreck (1985) estimated that less than 14% fly more than 20 m above the ground. If so, most beetles disperse under or within the forest canopy. Assuming on average circular infestation spots, this implies that spot size and immigration per spot unit area should be negatively correlated as the beetles probability of intercepting a spot will be proportional to the spot's linear dimensions rather than its area (Bowman et al., 2002; Englund and Hambäck, 2007).

Changes in the size of infestation spots with time in relation to the size of local *I. typographus* populations have only been addressed in a few studies. Schroeder and Lindelöw (2002) found an almost perfect linear relationship between numbers of colonised wind-felled spruces in storm gaps and numbers of trees killed in the following four years in southern Sweden. However, only five localities were surveyed in their study, and the size of the local population did not vary substantially. In a well-replicated study in Finland, covering sites with large variation in local population sizes, Eriksson et al. (2007) found that the number and size of wind-felled trees in storm gaps were the most important factors influencing subsequent tree mortality. However, the tree mortality was low and only observed in 27% of the study sites. In contrast, in the present study we analysed the tree mortality caused by local populations of *I. typographus* produced in wind-felled trees after a large-scale storm disturbance, covering storm gaps with a wide range of sizes during an intensive outbreak lasting several years. For this, we used data from a previous analysis of the importance of storm gap size (expressed as numbers of storm-felled spruces) and landscape variables for the colonisation of wind-felled trees by *I. typographus* (Schroeder, 2010). At the start of the present study the gaps studied by Schroeder (2010) hosted local beetle populations, produced in the wind-felled trees, that varied in size by a factor of almost three. We recorded the number of trees killed (i.e. spot growth) during the following five years around 35 storm gaps. We also included some additional gap variables in the analyses that have been shown to influence tree mortality (Eriksson et al., 2007). We had no information about populations in the surrounding landscape, thus we included forest variables reflecting the amount of *I. typographus* habitat (cf. Schroeder, 2010).

From a management perspective, risk assessment protocols providing reliable predictions of local tree mortality based on the size of local populations would be highly valuable for several applications. Firstly, after large-scale storm disturbances it is not generally possible to salvage all wind-felled trees before the emergence of the new generation of *I. typographus*. In such cases a risk assessment of tree mortality could provide useful indications of the storm gaps that should be cleared first. Appropriate protocols could also be valuable if storm disturbances occur in protected areas, e.g. national parks and reserves, where wind-felled trees are generally retained to promote biodiversity. Such areas often host rare species, which require the presence of mature spruce forest. Here, tree mortality risk assessments would be helpful for determining likely effects of possible management operations. In some cases, when the risk of major tree mortality is high, an appropriate option could be to remove some of the wind-felled or colonised trees, or otherwise make them unsuitable for bark beetle reproduction.

In the present study we addressed the following questions: (1) How does local population size in wind-felled trees influence tree mortality in the following years? (2) What additional storm gap and landscape variables influence tree mortality? (3) How does the tree mortality compare with the results of earlier studies?

2. Material and methods

The study was conducted in southern Sweden within a 1.8 million ha area in the counties of Kronoberg, Jönköping and Kalmar (Fig. 1). Approximately 80% of the study region is covered by forest, mostly managed for timber production by thinning and clear-felling. The stands are generally one-layered (i.e. even aged). Approximately 5% of the forest is set-aside for nature conservation purposes. Norway spruce and Scots pine *Pinus sylvestris* L. are the dominant tree species. The temperature in the study area was exceptionally high in 2006 with a total thermal sum (>8 °C) of 1100 day-degrees, in comparison to the mean of 2005, 2007 and 2008 (approximately 900 day-degrees) (Långström et al., 2009). In addition, the sum of precipitation was somewhat lower in May-Aug 2006 (245.7 mm) in comparison to the mean precipitation of the other years (364.2 mm, SD ± 81.5 mm) (SMHI-Swedish Meteorological and Hydrological Institute).

In January 2005, southern Sweden was hit by the storm Gudrun, which felled trees with a total volume of about 70 million m^3 (Svensson, 2007), of which about 80% were Norway spruces (Anonymous., 2006). About 8 million m^3 of wind-felled spruces remained in the forest during the first summer after the storm,