Forest Ecology and Management 260 (2010) 146–154

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Gap partitioning among temperate tree species across a regional soil gradient in windstorm-disturbed forests

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ARTICLE INFO

Article history:
Received 29 December 2009
Received in revised form 5 March 2010
Accepted 10 April 2010

Keywords:
Disturbance ecology
Forest management
Niche differentiation
Distribution models
Canopy gap
Natural regeneration

ABSTRACT

Canopy closure and soil characteristics are commonly used to explain regeneration distribution at local and regional scales, although very few studies take both factors into account. The combination of environmental variables defined at broad and local scales is necessary to provide regeneration distribution models with a small resolution (tree scale) that are valid on a large spatial scale (regional scale). Our aim was to quantify how gap partitioning among tree species at the seedling stage varies across large soil and stand type gradients. Regeneration inventories performed 5 years after gap creation were used to analyse the combined effects of soil type, stand type, and position within canopy gaps on the regeneration development of eight western European broadleaved species: *Acer campestre*, *Acer pseudoplatanus*, *Betula pendula*, *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus* sp., and *Salix caprea*. A clear pattern of gap partitioning among the eight species was observed. All species had higher density at the gap edge except birch and willow showing the highest presence in gap centres. For all species, the probability of presence of tall seedlings (height > 0.5 m) increased from gap edge to gap centre. Small seedlings presented the opposite trend except birch and willow. Soil pH influenced probability of presence for each species, but did not affect the pattern of gap partitioning among species. Both local (location within the gap) and regional (soil pH and stand type) scale factors affect recruitment distribution and are thus necessary to predict seedling distribution. The models developed may be used to determine the optimal gap size in order to obtain a given species composition according to soil and stand type conditions.

1. Introduction

Tree species habitat modelling studies seek correlations between environmental characteristics and tree species presence. Two main types of approaches have been developed, both based on the niche theory (Grubb, 1977) but applied in different contexts:

(A) Broad-scale approaches, applied at regional or continental scales, which belong to the field of plant science, focus on worldwide patterns. Species distribution is usually modelled as a function of climatic, topographic, geologic, or edaphic variables, which are postulated to exert a prominent effect on species' natural distribution (Guisan and Zimmermann, 2000; Willis and Whittaker, 2002). In most models, no distinction is made among the different developmental stages (Collins and Carson, 2004). However, it has been clearly stressed in the concept of regeneration niche (Grubb, 1977) that species–environment relationships vary with tree life stage. Consequently, seedlings have different requirements from adults and may therefore have different distribution patterns from adults (Stohlgren et al., 1998; Collins and Carson, 2004).

(B) Local-scale approaches, applied at forest or stand scales, are intensively used in forest science and study local processes. Species presence is analysed in relationships with locally defined variables such as stand structure or disturbance characteristics (Bugmann, 2001). These studies often distinguish the different developmental stages (Bugmann, 2001; Busing and Mailly, 2004).

Tree seedling distribution results from the conjunction of variables defined at different spatial scales (Grubb, 1977). Soil factors are important drivers of community composition (Aerts and Chapin, 2000; Willis and Whittaker, 2002). Specifically, soil pH strongly determines microbiological activity (Fierer and Jackson,

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doi:10.1016/j.foreco.2010.04.013

2006) as well as plant communities (Roem and Berendse, 2000) and is correlated with large-scale soil variability ranging from acidic soils on siliceous substrates to calcareous soils with high pH values. The response of tree seedling species to soil nutrients has been studied in controlled garden and greenhouse experiments (Walters and Reich, 2000). However, studies exploring the effects of a wide soil resource gradient on tree regeneration processes in natural temperate forest conditions are less frequent (Bigelow and Canham, 2002). Because seedlings are associated with the same soil types as mature trees, studies have focused on the adult stage or on all stages of the tree cycle together (Finzi and Canham, 2000).

In temperate forests, canopy gap opening is a major process determining regeneration development (Runkle, 1982) and a vast literature exists on the effects of canopy gaps on tree recruitment patterns (Harcombe et al., 2002; Kwit and Platt, 2003). The degree of canopy opening is correlated with many abiotic (e.g., light availability, soil and air temperature, air vapour pressure deficit, soil nutrient and water content) and biotic factors (e.g., humus quality, micro-flora and micro-fauna, herbivory) which are known to influence tree seedling establishment and development (Clark et al., 1999; Cote et al., 2004; Diaci et al., 2008). According to the gap partitioning hypothesis, gap opening favours seedling recruitment for all tree species, but differences among species in their responses to environmental gradients running from intact canopy to gap centre result in local-scale spatial variation in tree recruitment species composition (Denslow, 1980). The successive steps of seedling recruitment (seed rain, seed germination, seedling establishment and development) have all been shown to have species-specific distribution patterns within and around canopy gaps (Degen, 2006), creating the base of the gap partitioning effect. According to the seed–seedling conflict defined by Schupp (1995), seedling distribution is determined first by a heterogeneous pattern of seed dispersal and second by environmental variation influencing seed germination, seedling survival, and growth (Battaglia et al., 2004).

With the exception of Grogan et al. (2003) and Ediriweera et al. (2008), who analysed tree regeneration in relationships with soil characteristics (nutrients, pH, texture, and moisture) and canopy opening, very few studies have combined factors defined at local and at broad spatial scales to predict tree regeneration pattern. The main objectives of this study are: (1) to quantify how gap partitioning within gaps according to distance to edge among tree species at the seedling stage varies across large soil and stand type gradients, and (2) to establish models to predict the probability of seedling presence in gaps of different sizes located in different soil and stand types. The study is based on data extracted from a long-term project examining tree seedling and vegetation dynamics in gaps 5 years after windstorm opening, in northeastern France. The study focuses on eight broadleaved species commonly found in western Europe.

2. Materials and methods

2.1. Study sites and gap selection

The study was conducted in northeastern France, in the Lorraine region, which is part of the oceanic climatic domain with slight continental influences. Mean monthly temperature ranges from 0.8 °C in January to 17.5 °C in July. Precipitation is evenly distributed throughout the year with an annual mean of 947 cm. The main forest types are semi-natural broadleaf (*Quercus petraea*, *Quercus robur*, *Fagus sylvatica*, and *Carpinus betulus*) stands and conifer plantations.

Regeneration inventories extracted from a larger study on vegetation dynamics in gaps created by 1999 storms Lothar and Martin, across large gradients of soil type, stand type, and gap size, were used. Thirty-eight study sites were selected in 35 forests in Lorraine, representing 107 gaps (Table 1). All study sites were located in the 5.02–7.61°E and 48.06–49.04°N range and between 200 and 450 m a.s.l. Study sites were situated in regular high forest stands having 10–50% of their surface area damaged. No silvicultural treatments had been performed since the storms.

Table 1
Sampling design: number of gaps sampled in different soil types and stand types, representative of forests in northeastern France.

Stand type class	Soil type class				Total
	Calcareous	*Eutrophic*	*Loamy*	*Sandstone*	
Oak	7	13	16	1	37
Beech	3	3	5	13	24
Mixed broadleaf	11	8	4	2	25
Coniferous	13	2	2	4	21
Total	34	26	27	20	107

Three gradients were taken into account to select the study sites and the gaps within the sites. The first was the soil gradient varying from acidic sandstone substrate to calcareous limestone substrate. The pH value of the upper organo-mineral A-horizon ranged from 3.8 for gaps in acidic conditions to 7.9 for gaps in calcareous soils. The second gradient, stand type, was split into two classes: broadleaf and conifer stands. The third gradient, gap size (defined as the ground area within a canopy opening extending to the bases of the dominant trees that were contiguous with the surrounding stand, following Runkle (1981)), ranged from 86 to 6389 m^2 and was split into three gap size classes (small <840 m^2; intermediate, between 840 and 1500 m^2; large > 1500 m^2). In each study site, three gaps (one in each gap size class) were pre-identified on orthorectified aerial photographs, and their actual size calculated from field measurements (location of the surrounding trees). For each pre-identified gap, if gap size did not correspond to the target size, another gap was identified on the aerial photographs, and measured. No criterion for gap shape or for regeneration development was used to select the gaps. Twenty-five percent of the gaps sized less than 840 m^2, and 25% sized more than 1700 m^2. The average distance between the gaps within each study site was approximately 280 m with a maximum value of 2863 m and a minimum value of 6 m. Standing trees that were not contiguous with the surrounding forest canopy were included in the gaps.

2.2. Plot selection

For each gap, six to thirty-eight edge trees according to gap size (on average 12 trees) were selected and located by measuring their azimuth and distance to a reference point, geographically positioned using a GPS (GeoExplorer II Trimble®).

The edge trees were used to map the gap perimeter. Two perpendicular line transects, NNE–SSW (25–225 grads) and ESE–WNW (125–325 grads), passing through the gap barycentre were placed in each gap (Fig. 1). The transects crossed the gap and extended up to 6 m into the surrounding stand. A series of 2.01 m^2 circular plots (0.8 m radius) were placed at the gap barycentre and along each of the two transects. Plots were centred on the transects and were placed at 6 and 12 m intervals on the NNE–SSW and ESE–WNW transects, respectively (except for gaps larger than 30 ares, where plots were also placed at 12 m intervals on the NNE–SSW transect). The NNE–SSW transect was more densely sampled to capture the effects of the light gradient within the gap, which is more pronounced along a NNE–SSW than along a ESE–WNW direction (Diaci, 2002). When placing the plots, if adult trees or stumps were present at the plot location, the plot was moved 1 m along the transect in order to avoid any adult tree or stump within the plot. The plots were not moved if dead branches were present on the soil or if pits or mounds occurred. This design resulted in 1266 2 m^2 plots across