Research Note : Effects of landscape structure on seed dispersal of fleshy-fruited species along forest edges

RESEARCH NOTE

Effects of landscape structure on seed dispersal of fleshy-fruited species along forest edges

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Summary

1 Many plant species with fleshy fruits rely on birds for seed dispersal, yet little is known about how landscape structure affects bird-dispersed seed rain. This study investigates both the variation in seed rain along forest edges, and the attributes of the sites and the adjacent landscape that might influence it.

2 Along nine forest edges in the Swiss Jura near Olten the seed rain was measured with 450 traps during seven months. In addition, the specific species composition and the structure of the edges were recorded. The adjacent landscape within a radius of 200 m was analysed with a geographic information system (GIS).

3 Bird-dispersed seed rain correlated positively with the spatial structure of the edges studied, and with the length of the forest edges in the adjacent landscape within a radius of about 100 m. No other attribute of the investigated sites and their surroundings contributed significantly to the variation in seed rain. Since these results are only based on one vegetation period and on a small sample size, further investigations are necessary.

4 The results of this study have consequences for future land use planning, and show that evaluation of forest edges should include adjacent habitats. The data on seed rain indicate a considerable potential of the edge communities to recover from disturbance and to increase in species richness over time.

Keywords: edge effects, frugivorous birds, GIS, habitat structure, seed rain

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Introduction

Forest edges are a focus of both ecological research and conservation efforts, probably because progressive destruction and fragmentation of habitats have led to the creation of more and more forest edges in some areas (Saunders *et al.* 1991), whereas in other regions they have disappeared due to recent plantations or abandonment of adjacent farmland. Forest edges are transition zones between adjacent habitats. They tend to have distinctive microclimates, and are generally rich in species and microhabitats (Dierschke 1974; Coch 1995; Murcia 1995). The value and potential of forest edges have been thoroughly described, e.g. for Switzerland and Bavaria, and keys have been developed for their evaluation and for conservation (Schütz *et al.* 1993; Richert 1996, and references therein). Edges of new plantations are other objects of interest, especially in restoration schemes which aim to create a more diverse vegetation. For this purpose, existing edges of several forest types have been studied as templates for improving the poorly developed edges. Spontaneous development of new sites is often slow (10–20 years), but it can be accelerated by sowing or planting shrubs and by cutting adjacent forest trees to reduce shading (Richert & Reif 1992; Krüsi *et al.* 1996; Richert 1996).

So far, the majority of research on forest edges has been descriptive. Experimental studies, e.g. on seed rain, germination and establishment of new seedlings are, with a few exceptions, missing. Moreover, the projects cited often do not include the functional significance of the surrounding landscape (but see Richert 1996), although both issues are highly important for evaluation and future development of edge habitats.

Forest edges in central Europe are rich in fleshy-fruited species (Ellenberg 1988), which are mainly dispersed by passerine birds such as thrushes and warblers (Snow & Snow 1988). Although edge effects on bird abundance are well known (Yahner 1988; Cieslak 1992), little attention has been paid to the consequences which higher bird density near forest and scrub margins has on bird-mediated seed rain (see Herrera 1985; Hoppes 1988; Willson & Crome 1989; Debussche & Isenmann 1994). This lack of information is surprising since there have been many studies of frugivory and seed dispersal in the last twenty years (Estrada & Fleming 1986; Fleming & Estrada 1993). It is also unfortunate because bird-mediated seed rain is important for the improvement of poorly structured forest edges (Richert 1996), for succession on forest clear-cuts (Gorchov *et al.* 1993), and during regeneration of disturbed sites (Robinson & Handel 1993). Since birds are highly mobile organisms their behaviour may reflect the structure of the surrounding landscape, their habitat preferences being determined partly by the pattern of adjacent habitats (Herrera & Jordano 1981; Kollmann 1994). However, the spatial scale over which such effects operate is not known.

The seed rain of fleshy-fruited species has been shown to reflect habitat preferences of frugivorous birds (Blake & Hoppes 1986; Levey 1988; Kollmann 1994; Kollmann & Pirl 1995). Therefore, seed rain integrates two important biological processes which both have a bearing on landscape planning (cf. Gottsberger *et al.* 1991): (1) habitat preferences and abundance of frugivorous birds, and (2) distribution and dispersal of fleshy-fruited plant species.

In this study we investigated the spatial patterns in seed rain, the total number and diversity of seeds, and the percentage of bird-processed seeds. The research questions are the following:

(1) Which is the relative contribution of the local vegetation (i.e. within 50–100 m^2) and the surrounding landscape to bird-mediated seed rain along forest edges?

(2) Which landscape features are important (percentage of forest, forest edges, type of agricultural land etc.)?

(3) Which distance shows a significant landscape effect?

Study sites and methods

STUDY SITES

In spring 1996 nine study sites were selected on the southern slopes of the Swiss Jura near Olten, Canton Solothurn (460–590 m a.s.l.; Olten: 8.7 °C mean annual temperature, 1156 mm annual precipitation; Walter & Lieth 1964). The landscape in that region is highly

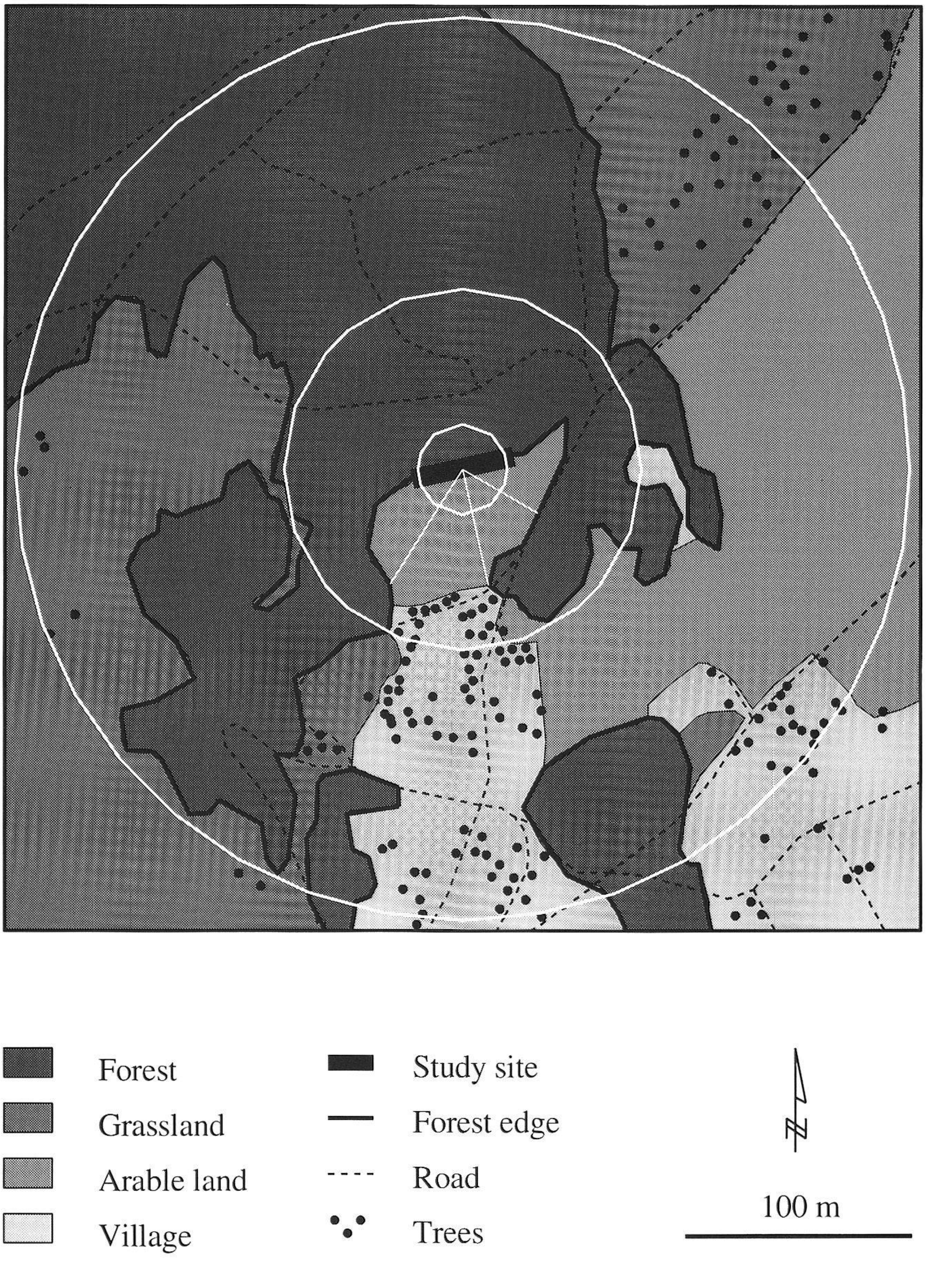

Fig. 1. The structure of the landscape around the Wangen site 6. The 20 m circle includes only the forest edge of the site itself. The 200 m circle is the largest which was analysed. Analyses of the spatial structure within the 80 m circle produced the strongest correlation between length of forest edges and seed rain. The distance to the nearest opposite forest edge was measured as an average for three angles to the site (45°, 90°, 135°).

diverse. There are several small villages surrounded by different types of agricultural land (arable, meadows, pastures and orchards) and border on extensive stands of forest which cover the middle and upper slopes of the Jura (Fig. 1). With one exception the study sites were arranged in pairs near four villages, with a distance of 100–500 m between sites and 2–5 km between the villages (Hägendorf, site 1/2; Rickenbach, site 3–5; Wangen, site 6/7; Lostorf, site 8/9; cf. Appendix).

All sites selected were south-facing on γ-marl limestone with a similar relief. The forest edges ran along calcareous beech forest or mixed oak-hornbeam forest and were composed of scrub communities belonging to the association Pruno-Ligustretum (Ellenberg 1988). These forest edges were old, undisturbed and rich in fleshy-fruited species (10–22 species), but clearly different in character compared to the adjacent habitats. Analysis of aerial photographs from 1951 revealed that the forest edges and the immediate surroundings have hardly changed for 45 years.

SEED TRAPS

The seed rain along the forest edges was recorded with 50 traps per site, spaced along a length of about 50 m (ten groups of five traps in each site). The traps were placed randomly beneath the shrubs along the forest edge, at about 1–2 m distance from the herbaceous fringe. All 450 traps were plastic buckets of 0.06 m^2 each, with drainage holes and covered to prevent seed predation by rodents. The same type had proved to be reliable in previous studies (Kollmann & Pirl 1995; Kollmann & Goetze, in press). The traps monitored seed rain during the main fruiting season from July 1996 to January 1997, they were checked monthly except in winter months when seed rain is low.

The collected seeds were determined with help of a reference collection and the keys of Bertsch (1941) and Beijerinck (1976). The seed rain consisted of two distinct fractions (Kollmann & Pirl 1995): (1) primary seed rain *(PSR),* due to berries falling directly off the bushes, and (2) secondary seed rain *(SSR),* after processing of fruit by birds. Primary seed rain is a rough estimation of differences in the abundance of fruit. Secondary seed rain, on the other hand, is proportional to the time spent by birds in a specific habitat (Pirl & Kollmann, in prep.), and can serve as an indicator for habitat preferences of birds. An even better indicator of habitat preferences is the *SSR* fraction of those species that did not fruit in the study site (SSR_{allo}).

DESCRIPTION OF THE FOREST EDGES

In autumn 1996 the frequencies of all fleshy-fruited species and of the fruiting individuals were recorded in 40 segments of 2 m each along 80 m of the forest edges studied. The total length of edge within a circle of 20 m radius centred on the site was measured (cf. Fig. 1). The vertical structure of the edge sites was described qualitatively.

LANDSCAPE STRUCTURE

The landscape structure in the surroundings of the forest edges was analysed with a geographic information system (GIS, ARC/INFO®) on the basis of digitized aerial photographs (1993 and 1994, 1:2000) and additional ground information. The survey was restricted to an area within a radius of 200 m around the study sites, since this is the distance over which seed dispersal by birds is most likely to occur (Kollmann 1994). In this area the following landscape elements were mapped: forest, forest edges, grassland, arable land, hedgerows, orchards, buildings and roads (cf. Fig. 1). Additional circles, with an increasing radius of 20–200 m (intervals of 10 m), were constructed to assess the density and distribution of the various elements within each segment. The distance to the nearest opposite forest edge was measured as an average for three angles to the study site (45°, 90°, 135°; cf. Fig. 1).

Results

SEED RAIN

The total seed rain of fleshy-fruited species amounted to 100–1000 seeds m^{-2} at the forest edges. Both primary seed rain *(PSR)* and bird-dispersed secondary seed rain *(SSR)* were significantly different among the sites (Table 1; ANOVA, $P < 0.001$), but not correlated (Spearman rank, $P > 0.05$). The basic composition of *SSR* was similar for all sites and was dominated by nine species which contributed 77% to the total *SSR*. The absolute number of fleshy-fruited species in *SSR* of an edge was variable (7–23 species of 24 species observed), but did not significantly correlate with the average *SSR* ($P > 0.05$). Of the total *SSR* (1846 seeds recorded) 22% were from species which were not found in fruit along the edges studied nor in its immediate surroundings (radius

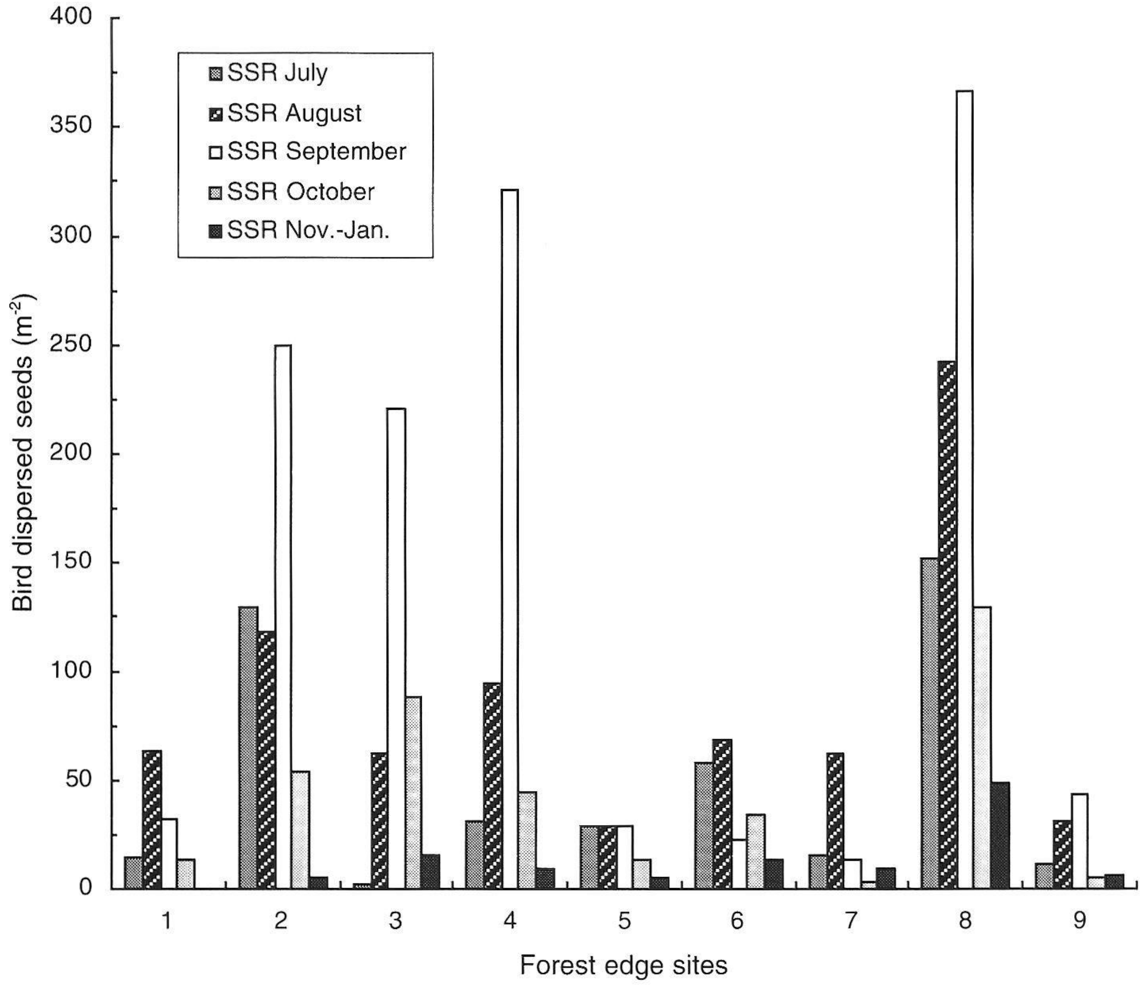

Fig. 2. *Temporal pattern of bird-mediated seed rain* (SSR) *at the nine forest edges in the Swiss Jura (July 1996–January 1997), means of ten values (five traps each) per site.*

Table 1. *Seed rain of fleshy-fruited species and site characteristics of the nine forest edges investigated. Seed rain was measured with 50 traps per site from July–January* (SSR, *bird-dispersed seed rain;* PSR, *primary seed rain; means* ± *1SE; ANOVA: **** P < *0.001). Average density of fleshy-fruited species was recorded for 40 segments (2 m) per site. Edge lengths are given for both the edges studied and the adjacent area (r_{80}, radius 80 m); percentage forest cover is calculated for the same area*

Study site	Seed rain (m^{-2})		Fleshy-fruited species	Forest edge length (m)		Forest r_{80}
	SSR	*PSR*	(m^{-1})	Site	Area r_{80}	(%)
8	940 ± 129	289 ± 84	3.46 ± 0.12	68	589	31
2	557 ± 110	99 ± 48	2.50 ± 0.12	40	231	54
4	502 ± 101	380 ± 107	1.66 ± 0.12	44	344	78
3	388 ± 112	696 ± 259	1.99 ± 0.10	45	334	84
6	196 ± 52	80 ± 49	1.58 ± 0.12	45	372	71
1	123 ± 39	175 ± 128	2.19 ± 0.13	39	132	53
5	106 ± 26	144 ± 52	3.40 ± 0.09	40	158	62
7	104 ± 15	83 ± 45	1.78 ± 0.08	42	185	59
9	97 ± 41	9.7 ± 4.3	2.29 ± 0.12	40	260	58
F	13.1***	3.7***	37.5***	–	–	–

around sites 20 m), i.e. SSR_{allo}. The ranking of the sites with respect to *SSR* remained similar during the seven months of the study. The total seed rain reached a maximum in September, and was rather small in July and in the winter months (Fig. 2).

STRUCTURE OF THE FOREST EDGES

The density of all fleshy-fruited species (1.6–3.5 species m^{-1}) and of those plants that were fruiting (0.4–1.0 species m^{-1}) were significantly different among the forest edges (Table 1; ANOVA, $P < 0.001$); so were Shannon diversity and evenness. Surprisingly, none of the four variables checked was significantly correlated with the average bird-mediated seed rain *(SSR)*. This indicates that other factors controlled the variation in seed rain along the edges, e.g. the structure of the edges or the diversity of the surrounding landscape. Indeed, both total *SSR* and SSR_{allo} were positively correlated with the horizontal structure, i.e. the length or curvature of the edges studied (Table 1; linear regression: *SSR*, $r^2 = 0.64$, $P = 0.01$; SSR_{allo}, $r^2 = 0.90$, $P < 0.001$).

EFFECTS OF THE SURROUNDING LANDSCAPE

The GIS analysis revealed strong differences between sites in aspects of landscape structure, e.g. the percentage of forest, grassland and human settlements (Table 1). Various landscape attributes were tested for correlation with average bird-mediated seed rain *(SSR)*. However, a significant correlation was only found between the total *SSR* (SSR_{allo}) and the length of forest and scrub edges in the surroundings.

The fit of the correlation between the total *SSR* and the edge length depended on the area considered (Fig. 3a). The positive correlation was significant for a radius of 20 m, i.e. the site itself. Extending the circle to 30–50 m, and subtracting the length of the site itself, revealed no significant correlation. However, the correlation was significant for a radius of 60–100 m. For annuli >100 m the relation disappeared again. This result was not an artefact of a site-specific species composition in *SSR*, since a similar, but less significant pattern was observed for *Cornus sanguinea*

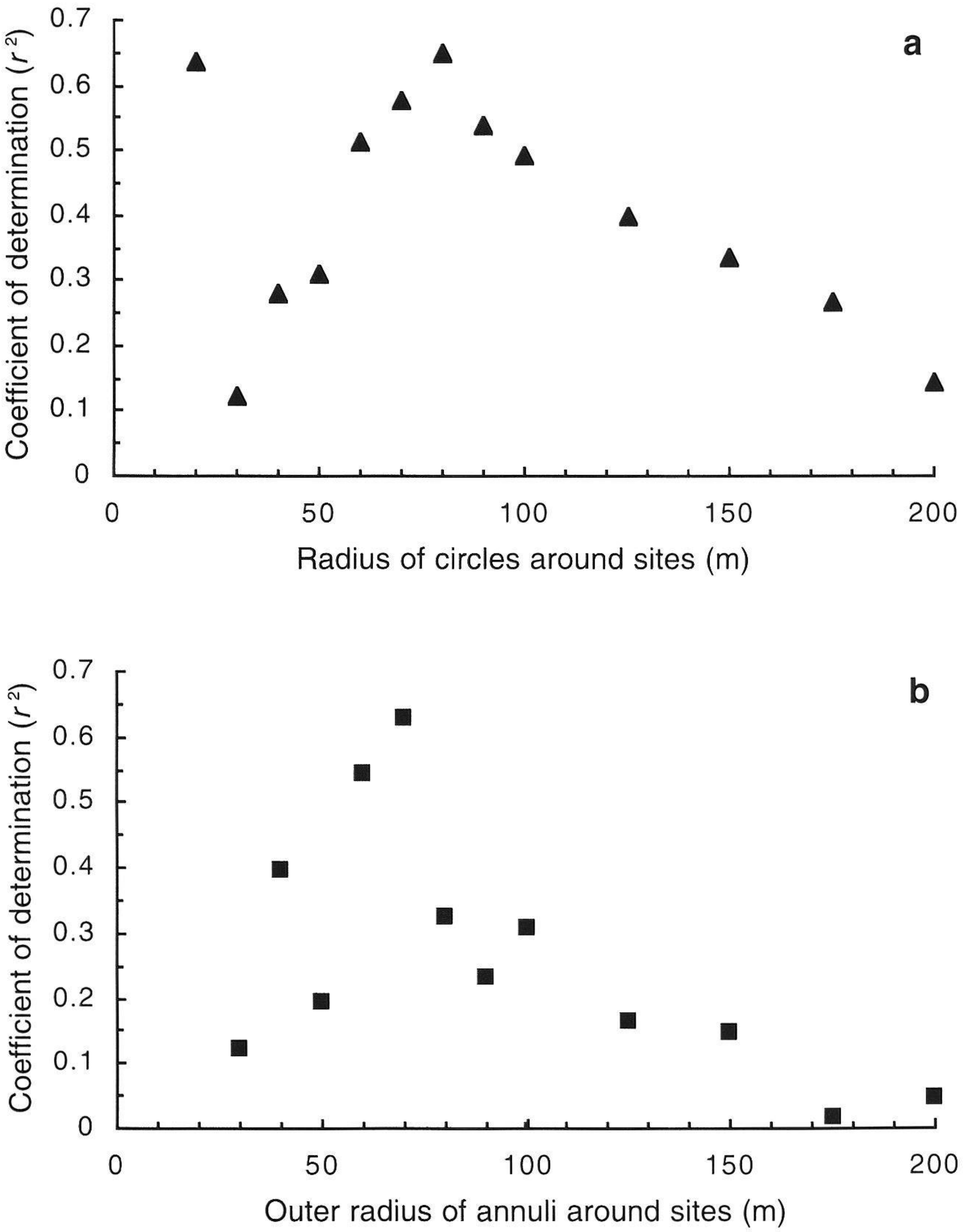

Fig. 3. *Regression fit for the dependence of average bird-mediated seed rain (SSR) on length of surrounding forest edges at nine sites. The edge length was measured (a) in disks with increasing radius around the sites (exclusive length of the study site), and (b) in annuli with increasing radius (20–30 m, 30–40 m, ...). For each distance a separate linear regression was calculated; $r^2 > 0.6$ was significant ($P < 0.05$). In (a) the result for a radius of 20 m reflects the effect of the horizontal structure of the edges investigated.*

and *Sambucus nigra,* the two most abundant shrub species.

In a second step we analysed which distances from the site made a significant contribution to the positive correlation with the total *SSR* (Fig. 3b). Only the annuli with a radius of 50–60 m and of 60–70 m contributed significantly. We suppose that this result was the effect of the nearest opposite forest edge. Indeed, the average distance to the opposite edge (55 ± 12 m, SE) was similar to the distance where the length of surrounding edges correlated with the *SSR*.

Discussion

SEED RAIN *VS* HABITAT PREFERENCES

The main objective of this study is to establish how landscape structure affects bird-dispersed seed rain *(SSR).* Surprisingly, forest and scrub edge length was the only landscape attribute that correlated significantly with the *SSR*. Since the abundance of frugivorous birds and fruit are especially high along forest edges in temperate regions (Baird 1980; Kollmann 1994), a positive correlation between edge length and bird-dispersed seed rain was expected. However, information about the spatial range of this effect has so far not been available.

The results of *SSR* suggest that both the horizontal structure of the edge site studied and the length of the surrounding edges contribute to the variation in bird-dispersed seed rain. Various explanations seem plausible. Firstly, the correlation of edge length and *SSR* over a distance of 50–100 m could simply reflect the average distance to the nearest opposite forest edge. Secondly, the correlation could indicate average flight distances of the relevant passerine birds. Finally, it could also be the landscape structure which is most preferred by frugivorous birds. Since information on these questions is scarce, further observations and experiments are needed.

PRACTICAL CONSEQUENCES

The preliminary findings have implications for landscape planning because they emphasize the significance of spatial structures of forest edges (Coch 1995), and suggest a distance over which edges might be connected by bird-mediated seed dispersal. This should affect optimal spacing of planted forest edges, hedgerows and scrub. The data on seed rain also show a considerable potential for the development of recently created forest edges and hedgerows. Richert (1996) actually reported that adjacent old forest edges enhance the colonization of younger ones over a distance of 50–100 m. Even the edges of dense spruce plantations can increase in species diversity due to seed dispersal by birds; in this study the *SSR* along a plantation near site 3 & 4 averaged 25–30% of the seed rain observed in the adjacent deciduous sites (Kollmann, unpubl.). However, we agree with Krüsi *et al.* (1996) that trees and shrubs along forest edges need to be cut to improve seed and seedling survival (Kollmann 1994).

FURTHER RESEARCH

Several critical points remain to be investigated. The results of this study have to be confirmed at different sites. It would also be desirable to test, e.g. by line taxation or mist netting, if abundance of frugivorous birds is actually higher at sites where the length of edges is high in the adjacent landscape. The conclusion that habitat preferences of birds and therefore bird-mediated seed dispersal depend on certain landscape attributes should also be checked for other habitat types, e.g. forest gaps, patches of scrub in abandoned grassland and hedgerows.

The high seed rain recorded along forest edges indicates a considerable potential of the edge communities to react to disturbance and to increase in species richness over time. However, high and diverse seed rain does not simply translate into seedling recruitment, since differential seed and seedling mortality might interfere (Herrera *et al.* 1994; Kollmann 1995; Kollmann & Schill 1996). Therefore, the spatio-temporal patterns of seed predation, germination and establishment must be investigated along forest edges to develop the best management scheme and to understand the impact of bird-mediated seed rain on succession of edge communities.

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Appendix

Location of the study sites

Village	Site	National Grid reference
Hägendorf	1	629.229 / 242.227
	2	629.177 / 242.924
Rickenbach	3	631.252 / 244.195
	4	631.293 / 244.292
	5	631.156 / 244.375
Wangen	6	631.656 / 244.482
	7	631.678 / 244.753
Lostorf	8	635.799 / 247.901
	9	636.140 / 248.126