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Distribution of Sorbus aucuparia (Rosaceae) regeneration in relation to trees in a subalpine spruce forest (W Carpathians, Poland)

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ABSTRACT: The distribution of rowan (*Sorbus aucuparia* L.) saplings was analyzed within and around a large windthrow in a subalpine spruce forest of Babia Góra National Park. Rowan sapling density was higher under the spruce canopy than in the open. Young rowans accumulated under trees in the understory of the spruce stand around the windthrow, and their density decreased with the distance from trunk bases. Seed dispersal by birds and spatial differentiation of ground vegetation are suggested as possible factors determining the distribution of rowan saplings. It is suggested that the rowan, a pioneer species, does not necessarily invade gaps in this subalpine forest but rather forms a bank of suppressed individuals in the understory, which are released after stand breakup.

KEY WORDS: canopy gap, regeneration, spatial structure, *Plagiothecio-Piceetum*

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INTRODUCTION

One of the most striking features of European subalpine spruce forests is the very simplified structure of tree stands in the optimal phase of their development. Monolayered and dense spruce stands cover large areas, as the optimal phase lasts 100–200 years and is the longest one in the development cycle (Korpel’ 1980; Mayer & Ott 1991). These stands often undergo catastrophic destruction caused by strong wind, hailstorms, snow loads and insect outbreaks (Korpel’ 1982; Fisher 1992). *Sorbus aucuparia* L., a short-lived and light-demanding deciduous tree (Ellenberg 1986; Kräuchi & Kienast 1993), is one of the most important pioneer species which develops in gaps and large disturbed patches and launches the succession toward spruce stands (Korpel’ 1980; Vacek & Tesar 1991; Fischer *et al.* 1990; Fischer 1992; Loch 1994; Reif & Przybilla 1995; Kooijman *et al.* 2000).

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In disturbed areas the rowan is often situated in the vicinity of snags and on windthrow mounds. Such a situation was reported from the Gorce Mts, where spruce stands had been destroyed by *Cephalcia falleni* Dolm. during its seven year outbreak (Witkowski *et al.* 1987; Loch 1994). A similar regularity was noticed in subalpine forest on Romanka Mt. in the Beskid Wysoki Mts (Holeksa *et al.* 1996). Occurrence of the rowan on windthrow mounds is a common phenomenon in Bayerischer Wald National Park (Fischer *et al.* 1990). It has been supposed that such a spatial pattern is a result of seed dispersal by birds which use snags and other elevated structures as perches.

However, gaps and large open areas are not the only places rowan occurs in the subalpine forest; it also grows under more or less closed spruce canopy. Phytosociological data show that the rowan forms a stable admixture in the understory of subalpine spruce forests in the Carpathians and Alps (Matuszkiewicz 1977; Ellenberg 1986). At the upper forest limit, rowan thickets cover considerable areas in different mountain areas (Borysiak 1978; Schaminee *et al.* 1992). There are no adult individuals of *Sorbus aucuparia* under spruce canopy, but its seedlings and saplings are widespread; however, their height rarely exceeds 130 cm (Celiński & Wojterski 1978; Jaworski & Karczmarski 1995; Reif & Przybilla 1995).

This paper examines the distribution of rowan saplings under a closed spruce stand around a large windthrow in order to determine its relationship with trees. In particular the study analyses *(1)* the density of rowan saplings under canopy and within windthrow, and *(2)* the spatial relation between saplings and spruce trees in closed forest.

Material and methods

Study area

The investigations were made in a subalpine spruce forest of Babia Góra National Park at about 1220 m a.s.l. The climate is cool with a mean annual temperature of 3.3°C, mean annual rainfall of 147 cm, and a snow-free period of 7 months (Obrębska-Starklowa 1983). All the climatic data refer to the meteorological station situated 30 m lower and 500 m east of the studied plots. The soils are mainly humus-iron podzols, iron podzols and podzolized rankers. They developed from Magurian sandstone with mudstone interbeddings (Adamczyk 1989).

The investigated forest represents a regional West Carpathian association *Plagiothecio-Piceetum* (Szaf., Pawł. & Kulcz. 1923) J. Mat. 1977, which is distributed in the Tatras and the highest parts of the West Beskid Mts (Matuszkiewicz 1977). The tree stand consists of Norway spruce *Picea abies* Karst. which is 100–270 years old in the investigated area (Jaworski & Karczmarski 1995; Holeksa 1998). Its density on three transects varied from 275 to 400 trees/ha, and the basal area ranged from 32.9 to 46.1 m^2/ha. The herb layer is patchy and usually dominated by bilberry *Vaccinium myrtillus* L. or ferns *Athyrium distentifolium* Tausch *ex* Opiz and *Dryopteris dilatata* (Hoffm.) A. Gray.

Field methods

Three transects were established at the edge of a large windthrow with several fructifying rowan trees situated within it more than 50 m from its edge. The windthrow appeared in 1970 over an area of 2 ha

(Gądek 1987) and has enlarged to about 5 ha since that time. The three transects were 20 m wide and their long axes were perpendicular to the border between the closed spruce stand and the windthrow. They were situated on the south, east and west sides of the windthrow. Transect I was 80 m long, with 3/4 of its area within the tree stand and only 1/4 in the windthrow. Transects II and III, 100 and 80 m long respectively, were equally divided between closed forest and open area.

The location of the spruces, the range of their crowns and the distribution of rowan saplings were mapped (1:100 scale) within every transect. Only saplings higher than 30 cm were mapped. The diameter of the spruces at breast height (1.3 m) was also measured.

Analysis of maps

To determine whether the rowan saplings are evenly distributed, the transects were divided into 4 m segments and the number of saplings was counted in each segment.

To compare sapling density in closed forest and within the windthrow, transects II and III were divided into 10 m^2 (4.0×2.5 m) subplots and average density was counted for the understory and the windthrow separately. There were 200 such subplots in transect II, and 160 of them in transect III. They were divided equally between closed stand and open area. Transect I was not considered in this analysis as it includes only a small area of the windthrow. The distributions of the number of saplings in the 10 m^2 subplots within the windthrow and under spruce canopy were compared with the Kolmogorov-Smirnov test.

The vertical projection of each spruce crown was divided into three zones – inner, middle and outer – as shown in Fig. 1 and their area was calculated. The shape of the crown projection was assumed to be an ellipse. The area of the whole crown projection and the area of each crown zone were summed for all trees in the closed forest of every transect.

The total number of rowan saplings was counted under the spruce crowns and outside the outer limit of their projection. The total number of saplings under three crown zones also was counted. Under random distribution the number of saplings under spruce crowns, outside them, and within the three zones should be proportional to their areal share. These null hypotheses were tested with the χ^2 test for every transect separately.

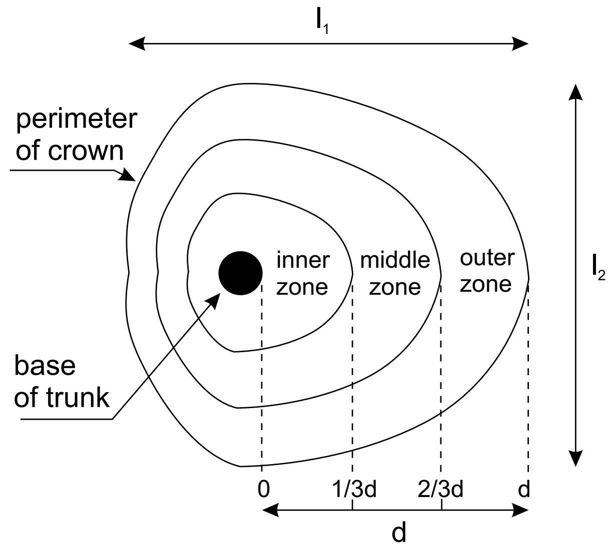

Fig. 1. Division of crown vertical projection into inner, middle and outer zones. l_1 and l_2 – diameters of elliptical crown projection; d – distance between trunk and crown perimeter.

Results

Rowan saplings were not evenly distributed along the transects. In transects I and II there were distinctly more saplings from the stand edge into the closed forest up to about 40 m. In transect III the difference between tree stand and windthrow was also clear, but saplings were most numerous in the area farthest from the stand edge (Fig. 2).

The density of rowan saplings was higher under closed spruce stands than within the windthrow. In transect II the difference was slight: 1.03 and 0.79 individuals per 10 m^2 under the stand and in the open area, respectively. In transect III the sapling density in the forested part was more than double that within the windthrow: 5.35 and 2.02 individuals per 10 m^2. The differences were significant for both transects (Kolmogorov-Smirnov test; transect II: $DN = 0.42$, $p < 0.001$; transect III: $DN = 0.5$, $p < 0.001$).

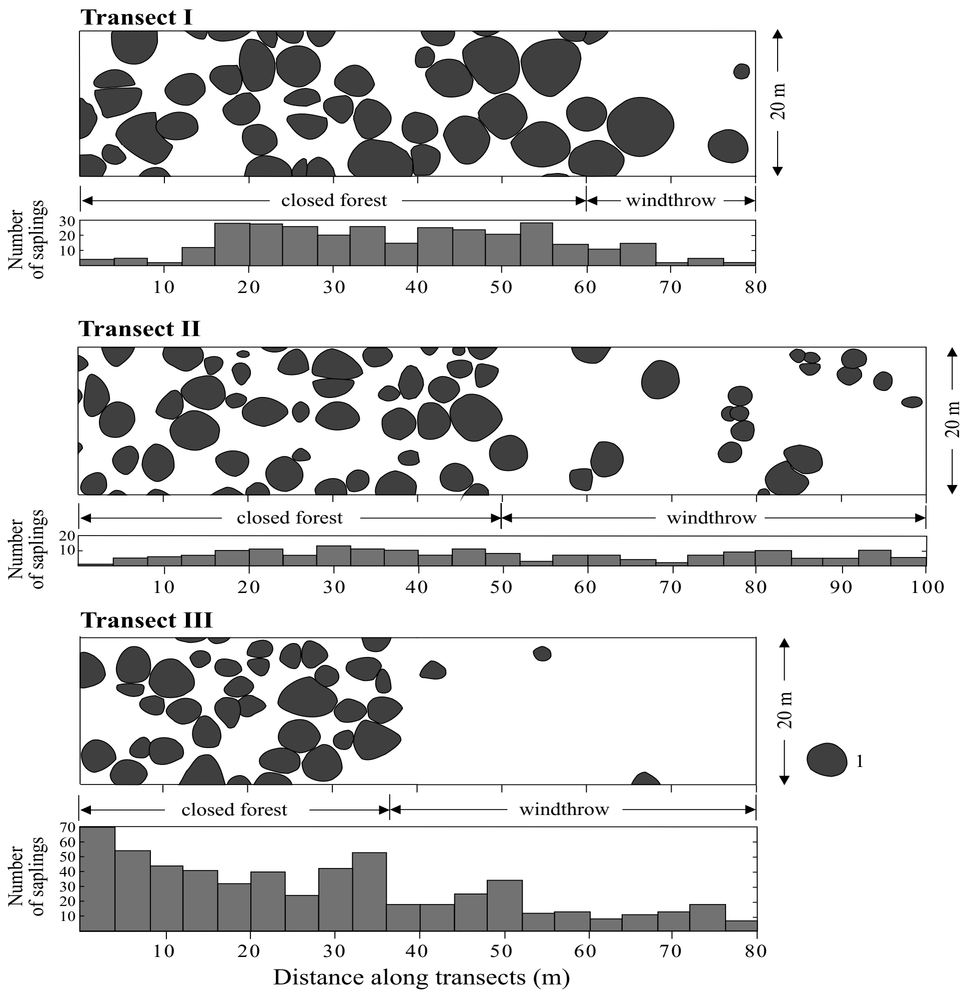

Fig. 2. Distribution of rowan saplings in closed forest and within the windthrow on three transects. Numbers of rowan saplings were counted for 4 × 20 m plots. 1 – projection of spruce crowns.

In transects I and II the density of saplings under spruce crowns was much higher than outside them. The differences were highly significant (transect I: $\chi^2 = 63.8$, $df = 1$, $p < 0.001$; transect II: $\chi^2 = 19.9$, $df = 1$, $p < 0.001$). In transect III the difference was small and not significant (Fig. 3).

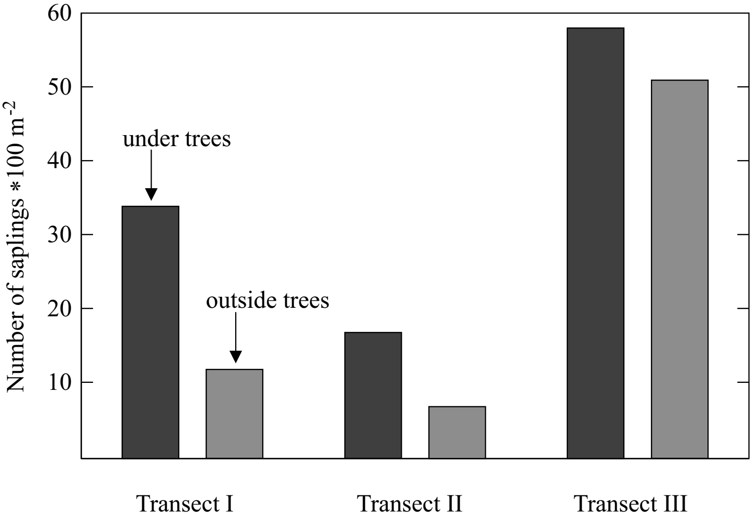

Fig. 3. Density of rowan saplings under and outside spruce crowns in closed forest of three transects.

Rowan saplings were not randomly distributed under spruce crowns. Their density decreased with the distance from the tree trunks (Fig. 4). In transect I, where the highest difference was noted, sapling density in the inner zone was three times that in the outer zone. The departure from a rectangular distribution against crown zones was significant in transect I ($\chi^2 = 42.4$, $df = 2$, $p < 0.001$) and in transect III ($\chi^2 = 26.8$, $df = 2$, $p < 0.001$). In transect II the difference was also considerable although not significant.

Discussion

The density of rowan saplings was highly variable in a fragment of subalpine spruce forest comprising a large windthrow and surrounding closed spruce stand. Although fructifying rowan trees were present only within the windthrow, regeneration of this species showed a clear connection with the understory of pure spruce stand. This result is consistent with the observations of Kasprowicz (1996), who noticed that the rowan is particularly abundant around large gaps and windthrows in the whole range of subalpine spruce forest on the Babia Góra massif.

Seed dispersal by birds appears to be one of the main factors determining the spatial pattern of rowan saplings. The fleshy and distinctly colored rowan fruits are eaten by

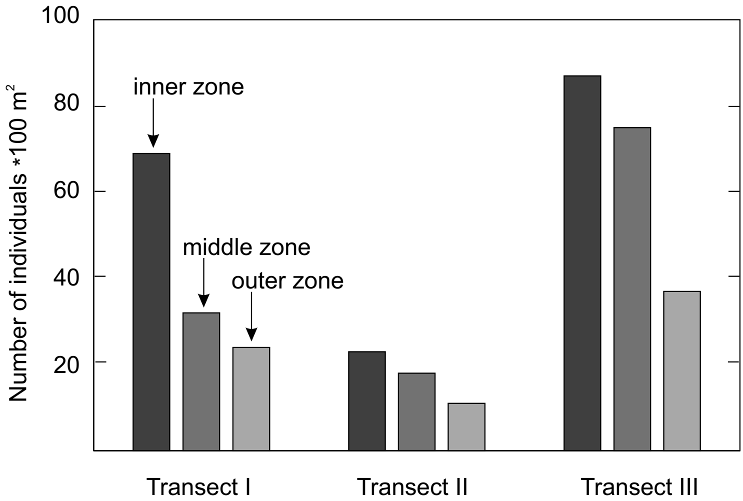

Fig. 4. Density of rowan saplings in three zones of vertical projection of spruce crowns in closed forest of three transects.

many frugivores (Bartkowiak 1970; Pulliainen 1978; Harmata 1987). Several frugivorous birds occur in subalpine spruce forests, but only species of large body size like *Turdus* spp. can be regarded as major rowan dispersers. *Turdus torquatus* is usually among the dominant species and *T. viscivorus* often occurs in considerable numbers (Głowaciński 1991; Głowaciński & Profus 1992; Saniga 1995). Feeding in gap centers and moving to the gap edge could be responsible for the observed sapling pattern. Such behavior of birds is probable according to Hoppes (1988), who investigated seed dispersal from a seed source situated in a gap center. He often observed two seedfall peaks: the highest near the seed source and the second one at the gap edge. Schupp (1993) demonstrated that *T. merula* and *T. viscivorus* usually selected closed stands as the post-foraging microhabitat and often flew more than 15 m from the feeding tree. *T. viscivorus* is one of the most effective dispersers as it often perches on tall trees more than 50 m from feeding trees (Schupp 1993). My results suggest that birds penetrate spruce stands up to 30–40 m from the edge. Beyond this distance a sharp decline in sapling density was observed in two out of the three transects.

Considering only the understory of spruce forest, it was demonstrated that the distribution of young *Sorbus aucuparia* is related to the spatial structure of the stand. There were more saplings under spruce crowns than between them, and sapling density was highest right around the tree trunks. A similar spatial relationship was observed in the Gorce Mts, where rowan saplings were usually situated around stumps over a large area of spruce forest cleared after a *Cephalcia falleni* outbreak (Loch 1992).

Perching on trees, snags and other exposed structures may result in clumped seed deposition and later the development of saplings close to them (Livingstone 1972; Willson 1986; McClanahan & Wolfe 1987). In a closed forest every tree plays the role of a perch, and can become a center of distribution of an ornithochorous plant. The distribution of *Sorbus aucuparia* in the understory suggests such a relationship. It can be also supposed that the birds perch close to the treetops or near the trunks, as the sapling density increased toward the tree bases.

Undoubtedly the high number of rowan saplings in the forest understory is an effect of seed dispersal by birds. There is rather no other way for these heavy diaspores to reach the forest interior, which is distant from the fruiting trees. However, the high density of young rowans under spruce crowns and particularly in the close vicinity of spruce trunks are not necessarily the effects of ornithochory alone. The distribution of rowan saplings seems to be thoroughly explained by seed dispersal, but it should be remembered that the observed pattern is also influenced by the spatial arrangement of safe sites for germination and suitable conditions for further development of young plants. Forests are mosaics of microsites which have different soil and biotic conditions. To a large degree this mosaic of soil conditions and understory vegetation is related to the distribution of trees and gaps (Wittig & Neite 1985; Moore & Vankat 1986; Andersson 1991; Pauley & Clebsch 1991). In subalpine spruce forest the distribution of trees and the spatial pattern of the herb layer are closely related (Parusel & Holeksa 1991). The herb layer of this forest consists mostly of patches dominated by single species, and *Athyrium distentifolium*, *Dryopteris dilatata* and *Vaccinium myrtillus* cover the largest areas. Patches of *Dryopteris dilatata* and *Vaccinium myrtillus* usually surround trees, and conglomerations of *Athyrium distentifolium* always avoid the immediate vicinity of tree trunks and develop exuberantly in gaps (Parusel & Holeksa 1991; Kasprowicz 1996; Holeksa 1998). It is possible that tall and dense clumps of *A. distentifolium* eliminate seedlings of *Sorbus aucuparia* as they usually constrain the development of young spruces and other plants (Parusel & Holeksa 1991; Reif & Przybilla 1995). Hytteborn and Packham (1987) and Lundqvist (1991) also found higher density of spruce seedlings and saplings below tree crowns than in gaps, and probably competition from the field layer was one of the causes of the observed pattern. Thus the association of rowan saplings with tree bases can also result from the herb layer's spatial differentiation. This relationship probably strengthens the effects of clumped seed dispersal.

The rowan is usually considered a pioneer species which develops after stand destruction (Fischer *et al.* 1990; Loch 1998; Kooijman *et al.* 2000). In light of my results, however, the presence of *Sorbus aucuparia* is not necessarily due to invasion of gaps after the breakup of stands. It can be present before stand destruction as young suppressed individuals which are released and form early stages of succession (see also Lund-Hoie & Andersen 1993). Phytosociological investigations suggest that the rowan often forms a bank of sparsely distributed suppressed saplings in subalpine spruce forest. Celiński and Wojterski (1978) made 41 relevés in spruce forest of Babia Góra massif. The rowan took part in the formation of tree stands in only two of them. It was present in the shrub layer in 18, and grew in the herb layer in all but three relevés. It can be assumed that this sample is unbiased with respect to the rowan as this species is of low diagnostic value (Celiński & Wojterski 1978). My own unpublished phytosociological data consists of 41 relevés randomly distributed over the old-growth spruce forest of Babia Góra massif. In this data set the rowan was present in the shrub layer in 14 relevés, and in the herb layer in 31 (Holeksa, unpubl.). A similar amount of *Sorbus aucuparia* in forest understory is reported from other areas (Matuszkiewicz 1977; Ellenberg 1986). This seedling and sapling bank probably can be supplemented by the seed bank, as rowan seeds are viable in the soil for several years (Granström 1987).

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