Seedling survival under conspecific and heterospecific trees: the initial stages of regeneration of *Sorbus aucuparia,* a temperate fleshy-fruited pioneer tree

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This study examined whether recruitment of *Sorbus aucuparia* under conspecifics and heterospecifics differs in: (i) seed-bank longevity, (ii) seedling emergence rate, (iii) seedling survival rate, and (iv) density-dependent mortality. I studied the first three cohorts of seedlings that emerged after the 2009 mast year using pairs of plots located under conspecific and heterospecific (Norway spruce, *Picea abies*) trees. The interannual pattern of seedling emergence did not follow the fruit production pattern. In 2010 and 2011, there was no difference in the density of emerged seedlings among the plots under rowans and under spruces. Survival of the 2010 and 2011 seedling cohorts was higher under spruces than under rowans. Under either tree species seedling survival was not correlated with the density of emerged seedlings. The survival pattern of rowan seedlings in subalpine spruce forest seems to follow the Janzen-Connell model in temperate forest.

Introduction

Survival of seeds and seedlings is often lower near the parent plant than at some distance from it (Augspurger 1984, Augspurger & Kelly 1984, Howe *et al*. 1985, Masaki & Nakashizuka 2002, Swamy & Terborgh 2010). The Janzen-Connell hypothesis suggests that host-specific natural enemies cause a disproportionate level of mortality of seeds and/or seedlings located under conspecific trees (Janzen 1970, Connell 1971). It has been invoked to explain the high level of species diversity in tropical forests, but a growing number of examples suggest that the ecological mechanism of higher mortality under maternal plants also operates in temperate forests (Shibata & Nakashizuka 1995, Packer & Clay 2000, Reinhart *et al*. 2005, Pigot & Leather 2008, Seiwa *et al*. 2008, Reinhart & Clay 2009, Yamazaki *et al*. 2009, but *see* McCarthy-Neumann & Kobe 2010). Increased mortality close to conspecific trees could be due to non-competitive negative density-dependent and/or positive distance-dependent mortality. For temperate forests, most studies highlight mortality caused by soil pathogens (Packer & Clay 2000, Reinhart *et al*. 2005, Seiwa *et al*. 2008), but mortality under conspecifics can also be due to the effect of herbivorous invertebrates (Pigot & Leather 2008) and vertebrates (Yamazaki *et al*. 2009).

For fleshy-fruited trees there is another difference between regeneration under conspecific trees and regeneration under heterospecific trees, besides the problem of escape from mortality under maternal trees. Propagules located under mother plants are mostly undispersed seeds still encapsulated in fruit pulp. Secondary metabolites in fruit pulp can inhibit germination (Cipollini & Levely 1997). The seeds of fleshy-fruited trees under heterospecific trees are bound to have been dispersed by animals. They have passed through an animal gut and are deposited on the ground in feces, without the fruit pulp. Frugivores can affect seed germination by scarifying the seed coat, separating the seeds from the pulp, removing germination inhibitors, and fertilizing with fecal material. These differences can have consequences for seed banking, seedling establishment, survival and growth (Robertson *et al*. 2006, Fedriani *et al*. 2012). Passage through the animal gut may increase seedling establishment and the growth rate, and it may be even more important than seed transport away from the mother plant (Fedriani & Delibes 2009). However, in the relationship between a plant and its disperser the plant does not always benefit at all stages of the recruitment process, in some cases recruitment of seeds ingested by an animal vector can be lower than that of non-ingested seeds with the pulp attached. Nevertheless, animals do enhance colonization of new areas by plants (Fedriani & Delibes 2011).

Pioneer trees achieve maturity and regenerate in tree-stand gaps, which are temporary habitats in forests. Pioneer plants that occupy such temporary sites reproduce early, as they are soon overcome by more competitive species; they rarely persist in one place for more than a generation (Hutchinson 1951, Howe & Smallwood 1982). Although a forest gap is a suitable site for a tree to reach maturity it can prove to be disadvantageous for regeneration as the situation changes. Schupp (1995) suggested that patches are characterized not only by present conditions but also by the probability of occurrence of particular temporal changes. In itself, temporal change at a patch is an integral component of patch quality. The suitability of a patch for plant recruitment can change depending on the succession stage, but the cumulative probability

of achieving reproductive age is crucial (Houle 1992, Schupp 1995, Rey & Alcántara 2000). Thus, many pioneer trees adopt a regeneration strategy that allows them to regenerate at sites where suitable conditions will occur in the future (colonization strategy; Howe & Smallwood 1982). Often they form a seed or seedling bank, waiting until a disturbance destroys a tree stand and improves the light conditions.

Rowan (*Sorbus aucuparia*) is a fleshy-fruited pioneer tree. Rowan occurs in subalpine Norway spruce (*Picea abies*) forests as one of two tree species. Spruce is dominant and rowan is considered a pioneer species. In disturbed patches in these forests, rowan often is the first species, forming short-lived thickets before spruce stands regenerate (Żywiec & Ledwoń 2008). Regeneration of rowan in gaps relies mainly on individuals from the seedling bank, emerging under the spruce canopy before it was disturbed (Żywiec & Ledwoń 2008). Seedlings persisting in the forest understory, waiting for a canopy disturbance, are essential to the rowan regeneration strategy (Żywiec & Holeksa 2012). Rowan is dispersed mainly by birds (Raspé *et al*. 2000). As a consequence of birds' foraging behavior, dispersed rowan seeds are deposited mainly under spruce crowns (Żywiec & Ledwoń 2008). If not dispersed the seeds are deposited under the crowns of maternal trees.

If birds dispersing rowan seeds perch preferentially on spruces and if mortality of rowan seeds and seedlings is higher under maternal trees, we should expect rowan seedlings in subalpine spruce forest to emerge and survive better under spruce trees than under rowan trees. To study this, here I compare seedling emergence and early survival under crowns of adult rowans (conspecifics) and spruces (heterospecifics). I examined whether recruitment under conspecifics and heterospecifics differs in: (i) seed-bank longevity, (ii) seedling emergence rate, (iii) seedling survival rate, and (iv) density-dependent mortality. I studied the first three cohorts of seedlings that emerged after the 2009 mast year. It is safe to assume that these cohorts originated mainly from seeds produced in 2009, as in the preceding year an almost complete absence of fruit production was recorded, and in the following two years fruit production was very low and

predispersal seed predation was high (Żywiec *et al*. 2012, 2013a).

Material and methods

Study species

Rowan (*Sorbus aucuparia*, Rosaceae, Maloideae) is a deciduous fleshy-fruited tree. It lives 100–150 years and reaches 15–20 meters in height (Hofgaard 1993). The fruits are 2–5-locular subglobose pomes (mean diameter 9 mm) containing one or two small seeds in each locule (Raspé *et al*. 2000). The seeds are dispersed by a wide range of animals, mainly birds (e.g., *Turdus* sp., *Sylvia* sp., *Garrulus glandarius*, *Bombycilla garrulus*, *Tetrastes bonasia*) and mammals (e.g., *Meles meles*, *Ursus arctos*) (Raspé *et al*. 2000). Frequently the seeds are eaten by larvae of the microlepidopteran *Argyresthia conjugella*, for which rowan is the principal host (Sperens 1997, Kobro *et al*. 2003). In subalpine spruce forest, rowan fruits ripen in August and September and the seedlings emerge the following June and July.

Rowan is distributed throughout almost all of Europe, Asia Minor, the Caucasus, western Siberia and North Africa. In the central European highlands it can be found from the foothills up to subalpine scrubland at 2000 m a.s.l. (Schaminée *et al*. 1992, Raspé *et al*. 2000). Rowan is generally considered a hardy pioneer species which only occasionally forms pure stands.

Study site

The study was done in a subalpine old-growth spruce forest on the Babia Góra massif (1725 m a.s.l.) in the Western Carpathians (Poland). The tree stands in the studied forest are composed of *Picea abies* with a sporadic occurrence of *S. aucuparia*. Small rowan thickets, a component of the forest dynamics, occur in gaps in spruce stands resulting from bark beetle outbreaks or windstorms (Żywiec & Ledwoń 2008). Under spruce stands, rowans form a persistent seedling and sapling bank (Holeksa & Żywiec 2005). In disturbed patches of these forests, rowan often is the first species forming short-lived thickets before spruce stands regenerate (Żywiec & Ledwoń 2008). When suppressed in the forest understory it grows slowly, while in gaps the growth rate is several times higher (Żywiec 2008).

Data collection

On the northern slope of Babia Góra between 1190 and 1250 m a.s.l., 47 pairs of plots (1 m²) were established. One plot of each pair was placed under a rowan crown, and the second one under a crown of the nearest spruce, within a few meters of the rowan. In 2010–2012, all new rowan seedlings were individually marked with numbered flags inserted in the soil near the seedlings. Survival of the 2010 and 2011 cohorts was monitored twice a year till July 2012.

In 2009–2011, 47 selected rowans (the same trees as in the plot pairs) were searched for fruits at the beginning of September before birds began to feed on them. Fruit production was evaluated using binoculars by counting the number of infructescences (corymbs with fruits) on individual trees. Five infructescences were randomly taken from each of those trees and all the fruits in them were counted. The fruit production of a tree was determined as the product of its number of infructescences and the number of fruits in an infructescence (average of the five taken) (Żywiec *et al*. 2012).

Data analysis

Interannual differences in rowan fruit production in 2009–2011 and in seedling emergence in 2010–2012 were analyzed with Friedman's test. Seedling density was calculated as their mean number in the square-meter plots under the rowan and spruce crowns.

A Wilcoxon test for dependent samples was used to compare the density of seedlings that emerged under the rowan and the spruce crowns. The non-parametric test was applied because the data deviated from a normal distribution. Comparisons were made for cohorts 2010, 2011 and 2012. The Wilcoxon test was used to find

out whether the consecutive cohorts of seedlings under rowans and spruces differed in density.

Correlation analyses were carried out to determine whether the density of emerged seedlings depended on seed supply from fruit fall or from seed dispersal. Spearman's rank correlation was used for the relationship between the density of emerged seedlings under rowan/spruce and the fruit production of the subject rowan in previous years. For the 2010 cohort one previous year was taken into account, for the 2011 cohort two previous years, and for the 2012 cohort three previous years. Spearman's rank correlation was also used for the relationship between the density of seedlings under rowan/spruce and the number of rowan trees within 40 meters. All rowan trees in the study area had been previously mapped (Żywiec et al. 2012) and the distances between plots and rowan trees measured with the ArcGIS 9.1. (ESRI) software. I took 40 meters as the distance for that procedure because earlier it was found that the density of rowan seedlings and saplings falls dramatically at distances greater than 40 meters from rowan trees (Żywiec et al. 2013b).

Differences in seedling survival between the plots under rowan and under spruce crowns were tested with the Wilcoxon test for dependent samples. The non-parametric test was used because the data did not follow a normal distribution, and contained numerous zero values. Differences were determined for the 2010 cohort in the first and second years of its life, and for the 2011 cohort in the first year of its life. Differences in the two-year survival of the 2010 cohort between the plots under rowans and under spruces were also tested. The Wilcoxon test was applied to find out whether the density of all seedlings in 2012 (sum of 2010, 2011 and 2012 cohorts) differed between the plots under rowans and under spruces. Interannual differences in seedling survival under rowans and under spruces were tested with ANOVA for dependent samples.

The relationship between seedling mortality and density was analyzed with Spearman's rank correlation, testing whether the first-year and second-year survival of the 2010 cohort was related to its density in 2010 and 2011 respectively, and if the first-year survival of the 2011 cohort was related to its density in 2011.

Results

Inter-annual variation of fruit production and seedling emergence

Fruit production differed markedly among the years in 2009–2011 (Fig. 1a; Friedman's test: χ^2_2 = 34.53, $n = 45$, $p < 0.0001$). In 2009 it was on average 3.7 and 3.9 times higher than in 2010 and 2011 respectively. Seedling emergence also varied among years (Fig. 1b; Friedman's test: $\chi^2_2 = 52.77$, $n = 47$, $p < 0.0001$) but the interannual pattern of this variation differed from that of fruit production. The number of seedlings in 2010 (mean = 7.6 m^{-2}) was almost the same as in 2011 (mean = 7.2 m^{-2}). In 2012 it was markedly lower: 23.8 and 22.6 times lower than in 2010 and 2011, respectively.

Emergence of seedlings and seed bank under rowan and spruce

In 2010 no difference was found in the density of emerged seedlings between the plots under rowan and under spruce (Fig. 2a; Wilcoxon's test: $p = 0.88$), and the same was true for 2011 (Wilcoxon's test: $p = 0.30$). The density of emerged seedlings did not differ between 2010 and 2011 under rowans (Wilcoxon's test: $p = 0.60$) or under spruces (Wilcoxon's test: $p = 0.68$) either. In 2011, most of the seedlings emerged from the seed bank, as fruit production in 2010 was much lower than in 2009. In 2012 the density of seedlings under rowans was on average four times higher than under spruces (Fig. 2c; Wilcoxon's test: $W = 2.7$, $p = 0.007$). However, for both plot types it was significantly lower than in the two previous years (Wilcoxon's test: under rowans 2012–2010 $W = 5.6$, 2012–2011 $W = 5.4$; under spruces 2012–2010 $W = 5.7$, 2012–2011 $W = 5.2$, $p < 0.0001$ for all comparisons).

The density of the 2010 seedling cohort under rowan trees correlated significantly with the number of fruits produced in 2009 by those trees (Spearman rank correlation: $r_s = 0.31$, $p = 0.04$). The density of the 2011 seedling cohort under rowans was not correlated with the number of fruits produced in 2010 but was correlated with
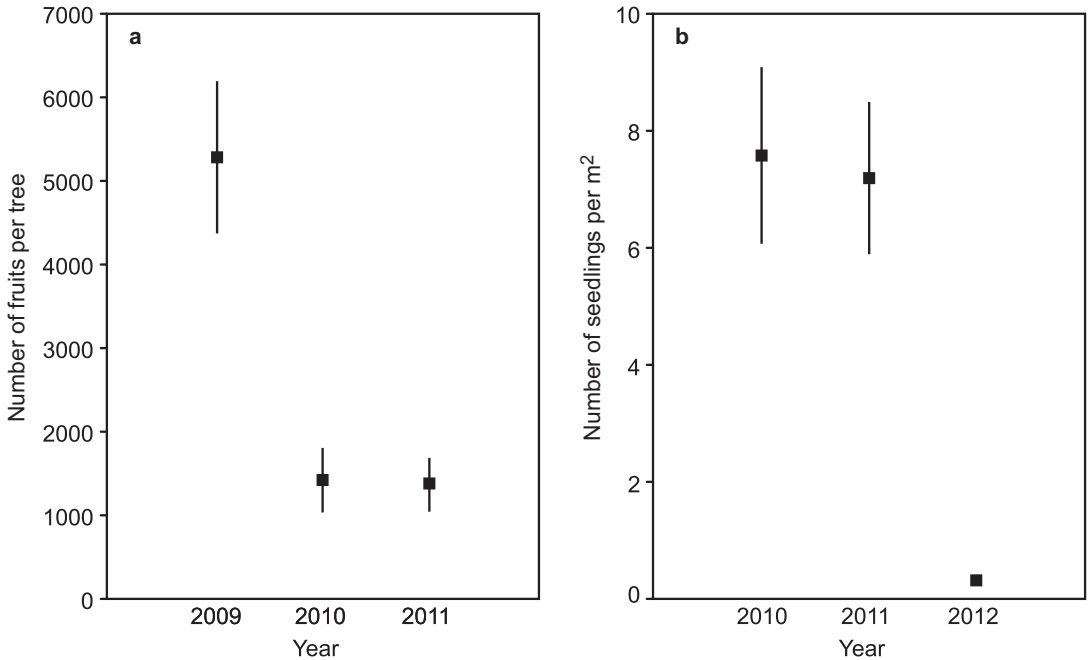
Fig. 1. (**a**) Rowan (*Sorbus aucuparia*) fruit production (mean ± SE) in 2009–2011, and (**b**) seedling emergence (mean ± SE) in 2010–2012. Fruit production was calculated for 47 subject trees and the number of seedlings was calculated for all 94 plots.
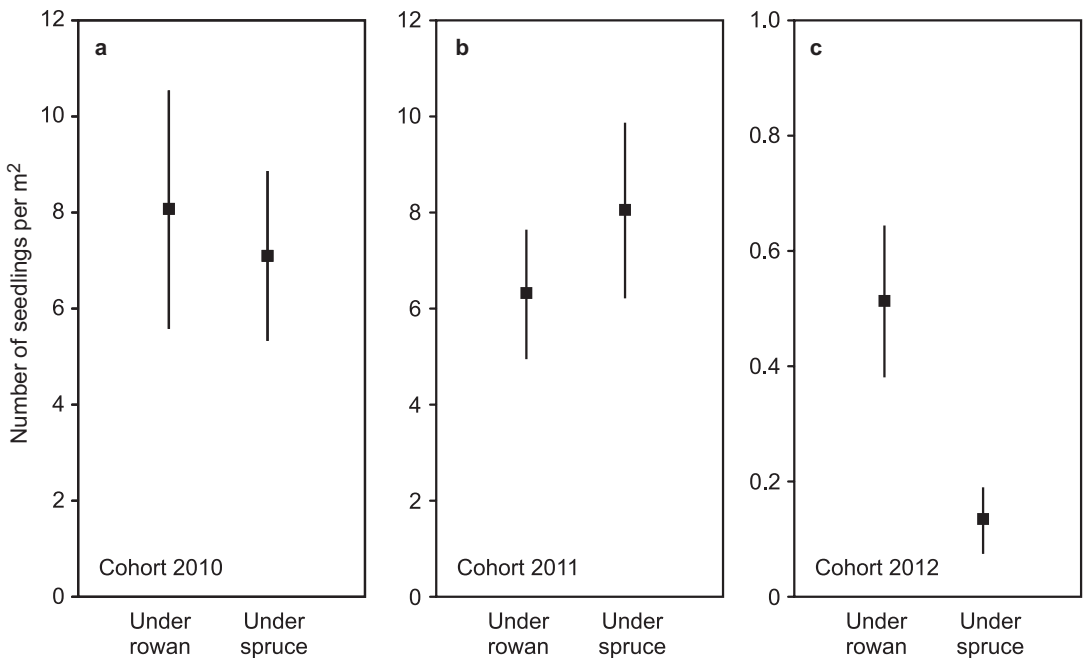

Fig. 2. Density of rowan (*Sorbus aucuparia*) seedlings (mean ± SE) under rowans and under spruces emerging in (**a**) 2010, (**b**) 2011 and (**c**) 2012.

the number of fruits produced in 2009 ($r_{\mathrm{S}} = 0.40$, $p = 0.006$). The density of the 2012 seedling cohort under rowans was correlated with fruit production in 2009 ($r_{\mathrm{S}} = 0.34$, $p = 0.02$) and in 2010 ($r_{\mathrm{S}} = 0.44$, $p = 0.002$) but not with fruit production in 2011. In all cohorts, seedling density under a spruce tree was not related to the fruit production of the nearest rowan tree.

Under spruces, seedling density of the 2010 and 2011 cohorts was significantly correlated with the number of rowan trees within a radius of 40 m (Spearman rank correlations: $r_{\mathrm{S}} = 0.45$, $p = 0.002$ for 2010, $r_{\mathrm{S}} = 0.35$, $p = 0.02$ for 2011). The density of the 2012 seedling cohort under spruces was not correlated with the number of rowan trees within 40 m. In all cohorts, seedling density under rowans was not correlated with the number of rowan trees within 40 m.

Survival of seedlings under rowan and under spruce

Survival of the 2010 and 2011 seedling cohorts in the first year after their emergence, and of the 2010 cohort in the second year after its emergence, was higher under spruces than under rowans, but those differences were significant only for the first-year survival of cohort 2010 (Fig. 3: Wilcoxon's test: $W = 3.0$, $p = 0.003$). Two-year survival of the 2010 seedling cohort was significantly higher under spruces than under rowans (Fig. 3; Wilcoxon's test: $W = 3.0$, $p = 0.003$). In 2012 the total density of the three 2010–2012 cohorts was on average 4.4 seedlings per m^2 under rowans and 6.2 seedlings per m^2 under spruces, but the difference between plot types was not significant (Wilcoxon's test: $p = 0.12$). Interannual differences in seedling survival both under rowans and under spruces were small and nonsignificant (ANOVA: $p > 0.35$).

Density-dependent mortality under rowan and under spruce

Seedling survival of the 2010 and 2011 cohorts in the first year after emergence, and the seedling survival of cohort 2010 in the second year after emergence, was not correlated with the density of emerged seedlings under rowans or under spruces (Spearman rank correlation: $p > 0.05$).

Discussion

In this study, I found large between-year differences in rowan fruit production and seedling emergence, but the interannual pattern of seedling emergence did not follow the fruit production pattern. Despite the big difference in fruit production between 2009 and 2010, seedling densities in the 2010 and 2011 cohorts were similar, both under rowans and under spruces. The differences in availability of viable seeds in 2009–2011 are even more pronounced if predispersal seed predation by *Argyresthia conjugella* is taken into account. It was previously found that seed predation by that moth varied considerably between years: 19.1% of fruits were infested in 2009, 75.4% in 2010, and 92.6% in 2011 (Żywiec *et al.* 2013a). As a result, production of uninfested fruits in 2009 was 12 times higher than in 2010 and 42 times higher than 2011.

Under rowans the number of emerged seedlings depended on the number of fruits produced by the subject tree, while seedling emergence under spruces was related to the number of conspecific (rowan) trees nearby. This difference reflects the different ways seeds arrived under rowans and under spruces. Seedlings under rowan trees most certainly originated mainly from seeds that fell under the mother trees in undispersed fruits. The lack of relationship between seedling density under rowans and the number of conspecific trees nearby suggests that birds do not disperse seeds when they forage in rowan crowns. This may be an effect of their avoidance of open spaces (Howe 1979). Rowan trees usually grow in canopy gaps and have sparse crowns which offer little shelter, exposing the birds to predators. Immediately after foraging they fly off to perch on dense-crowned spruces in the vicinity of seed sources (Hoppes 1987, Schupp *et al.* 1989). This pattern of foraging produces the relationship between rowan seedling density under spruce crowns and the number of nearby rowan trees.

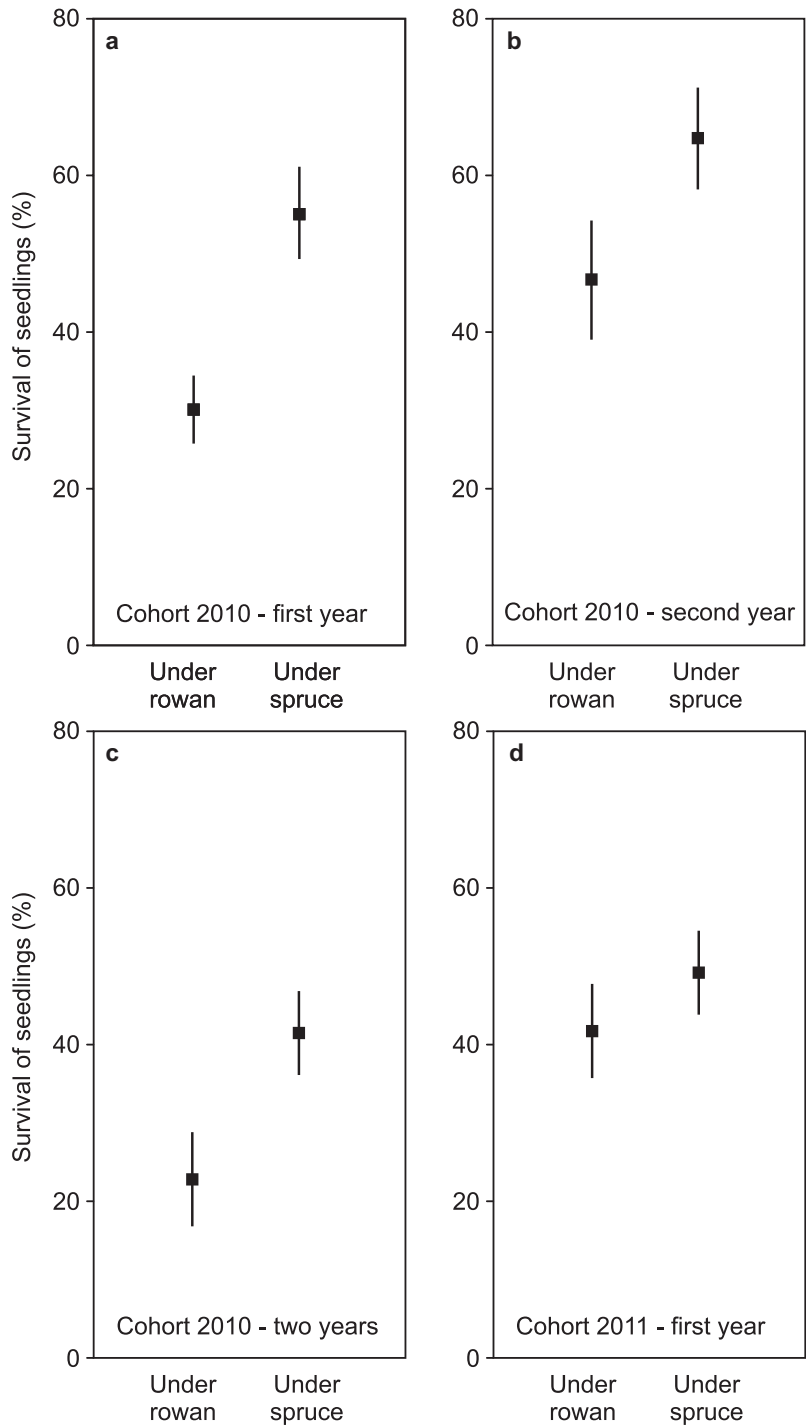The results strongly suggest that the 2011 cohort emerged mostly from seeds produced in

Fig. 3. Survival of rowan (*Sorbus aucuparia*) seedlings (mean ± SE) under rowans and under spruces: 2010 cohort in (**a**) the first year, (**b**) the second year and (**c**) after two years, and (**d**) 2011 cohort in first year.

2009. The presence of a short-term seed bank was indicated by the density of the 2011 cohort under rowans, which was not related to fruit production in 2010 but was positively correlated with fruit production in 2009. The 2011 cohort was as numerous as the 2010 cohort in spite of the great difference in fruit production between those two years. It is reasonable to infer that

rowan seedlings can emerge from the seed bank up to two years after seeds are deposited on the ground in subalpine spruce forest. One can ask if such a short-term seedling bank can be an important component of the regenerative strategy of rowan. However, even short-term seed banking can increase recruitment, as it can buffer annual fluctuations of seed production and/or unfavorable recruitment conditions (Hille Ris Lambers & Clark 2004). It seems important for rowan in subalpine spruce forests, where its interannual variation of fruit production is high and rowan seeds are heavily predated by *Argyresthia conjugella*, severely reducing the number of viable seeds (Żywiec *et al*. 2012, 2013a). The harsh climate of the subalpine zone can also reduce seedling survival in some years. It should be pointed out however that no between-year differences in seedling survival were found in the studied period.

Seedling emergence in the plots under rowans and under spruces did not differ in 2010 or 2011. Two opposing processes may have affected this result. On the one hand, the pool of seeds and in consequence seedling emergence usually decreases with distance from the mother tree as the distribution of seedfall usually is leptokurtic in relation to the parent tree (Howe & Smallwood 1982, Clark & Clark 1984, Wenny 2000, Gilbert *et al*. 2001). In the absence of data on rowan seed rain it was not possible to estimate the percentage of seeds that emerged, and it can be only suggested that while seed rain under rowans was higher than under spruces the percentage of seeds able to germinate was lower there. On the other hand, most rowan seeds deposited under mother trees were encapsulated in fruits. Seeds inside whole fruits may rot at higher rates than clean seeds do, and the pericarp can reduce seedling emergence (Fedriani *et al*. 2012). In a sowing experiment, Paulsen and Högstedt (2002) found that seedlings did not emerge from unopened rowan fruits; some seedlings emerged from opened fruits, but their emergence was considerably lower than emergence from seeds ingested by birds or extracted from fruits. In a study of another *Sorbus* species in field conditions, Yagihashi *et al*. (1998) reported that seeds from intact fruits did not germinate in the first spring due to the inhibi-

tory action of fruit pulp. They did not germinate in the second spring either when the fruit pulp was decomposed, having lost viability during the first summer. Our results on seedling emergence under rowans indicate that seeds were able to break the pulp inhibition and germinate in the first and second years after fruit fell, but emergence in the second year was slightly lower. Seeds deposited under spruce crowns emerged at a slightly higher rate in the second year. These findings seem to mean that in the second year the seeds dispersed by birds had better viability than those deposited under maternal trees.

The pattern of seedling emergence in 2012 differed from what was found for the two previous years. The density of emerged seedlings was considerably higher under rowans than under spruces. This may have been an effect of slightly higher seed bank longevity under rowans than under spruces, but it stands in contrast to the slightly higher rate of emergence from the seed bank under spruces in the 2011 cohort. The difference in seedling emergence in 2012 might also be explained by differences in seed dispersal patterns between years. The amount of fruits produced could affect the pattern of seed dispersal. In a year of low fruit production, rowans might attract fewer frugivores than in a heavy production year. During mast years, a high proportion of seeds are dispersed by migratory birds taking advantage of this abundant and easily available food. In years of low fruit production birds probably do not forage on rowans and search for other food sources available during their brief stopover in the Babia Góra region. Such an interpretation stresses the role of mast years for rowan seed dispersal, as a heavy production year may be necessary to attract seed dispersers. In regions where a zoochorous species must depend mainly on migratory bird populations, masting can be an adaptation not only to resist seed predation but also to support long-distance seed dispersal. The situation is different when seeds are dispersed by a local bird population; in such a situation, Herrera (1998) found that the percentage of the fruit crop removed from fleshy-fruited trees was independent of crop size or was even lower in large crops due to satiation.

The survival pattern of rowan seedlings in subalpine spruce forest follows the Janzen-Con-

nell model in temperate forest. Rowan seedling mortality was found to be distance-dependent. Rowan seedling survival was lower under rowans than under spruces a few meters away from them. The soil pathogens under rowan trees are one probable explanation for this. In studies of other Rosaceae species, soil pathogens were responsible for higher mortality under conspecifics (Packer & Clay 2000, Reinhart & Clay 2009). Another source of seedling mortality is herbivory. Vertebrate herbivores such as deer readily browse rowan seedlings (Heroldová *et al.* 2003) but the few-meter distance between seedlings under spruces and under rowans is unlikely to have affected that browsing activity much, and large herbivores would hardly have been attracted to tiny seedlings a few centimeters tall. The higher seedling survival under spruces than under rowans also demonstrates that light is not a limiting factor in rowan seedling survival, as insolation is greater under rowans growing in gaps than under spruces.

Differences in seedling survival between plots under conspecific and under heterospecific trees can also be affected by the condition of seeds deposited in the soil. Under rowans the deposited seeds were inside the fruits. According to Fedriani *et al.* (2012), seedlings often emerge later from fruits than from seeds extracted from fruit pulp. Seedlings emerging earlier can have higher survival than later-emerging ones (Shibata & Nakashizuka 1995). They have a longer period for growth, especially important in harsh mountain climate with its short growing season. The seedlings of the 2011 cohort under rowans would have been much less affected by the remains of fruit pulp than those of the 2010 cohort, as the pulp probably decomposed completely during the nearly two years following dispersal. In effect, first-year survival of 2011 cohort seedlings was only slightly and nonsignificantly lower under rowans than under spruces, and the differences in survival between the plots under rowans and under spruces were significant only for the first-year survival of the 2010 cohort.

Seedling survival affected the seedling distribution pattern. Three years after the mast year, rowan seedling density under conspecific trees was 1.4 times lower than under heterospecifics in spite of the fact that the density of all seedlings emerged in 2010–2012 did not differ between sites. The differences were not significant, however, and seedling density under rowans was still rather high. Thus, it seems that the previously reported absence of a second generation of rowans in tree stand gaps in subalpine spruce forest (Żywiec & Ledwoń 2008) is due not only to differences in seedling survival in the initial stages of recruitment but also to differences in mortality in later stages of development. Soil pathogens under conspecific trees can increase seedling mortality in the first years of life but can also slow their growth rate and in consequence impair their future development (Packer & Clay 2003).

Seedling mortality was not density-dependent under rowans or under spruces. One reason might be that seedling density was not high at either type of site, generally a few individuals per square meter. In most study systems, the density of seedlings is substantially higher under the mother plant than under heterospecifics, making it difficult to distinguish density-dependent from distance-dependent mortality without experiment (Packer & Clay 2000). In this study, no difference in seedling density between plots under conspecific and heterospecific trees was found, and mortality did not increase with the number of seedlings under rowans or under spruces. The conclusion to be drawn is that seedling mortality was only distance-dependent: it was higher under maternal rowans and lower under spruces. A lack of density-dependent mortality has been shown in other temperate (Houle 1992, Reinhart & Clay 2009) and tropical trees (De Steven & Wright 2002).

In subalpine spruce forest, rowans can reach tree size and produce seeds in tree stand gaps. This strong spatial relationship between gaps and adult rowan trees suggests that gaps favor the establishment and growth of young rowans. The second generation of rowans, however, has much less of a chance to complete the full life cycle in gaps, which can fill up with a new generation of spruces before that happens (Korpel' 1995). The sites suitable for rowan regeneration are under crowns of mature spruces, where they wait for canopy openings and preempt the free space before spruce has a chance to develop in

it. The results on seedling survival, better under spruces than under rowans, support that statement. Establishment of a rowan seedling bank under spruce is a prerequisite of future gap occupation. Rowan seedlings can persist in the forest understory for many years, due to their mechanism of sprouting, i.e. replacing dead stems with new ones (Żywiec & Holeksa 2012). In this context, dispersal of rowan seeds away from conspecifics growing in gaps to sites located under spruce crowns is a critical component of the rowan regeneration strategy.

Acknowledgements

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