

Population and individual level of masting in a fleshy-fruited tree

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Received: 3 November 2011 / Accepted: 2 May 2012 / Published online: 25 May 2012
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Abstract Masting is usually considered as a population phenomenon but it results from individuals' reproductive patterns. Studies of individual patterns of seed production and their synchrony are essential to an understanding of the mechanisms of masting. The aim of this study was to find the relationship between population and individual levels of masting. We examined individuals' contribution to masting, considering their endogenous cycles, interannual variability and associated weather cues, as well as inter-individual synchrony of fruit production. We studied masting of *Sorbus aucuparia* L., which in Europe is one of the most common trees bearing fleshy fruits and is strongly affected by a specialized seed predator. The data are 11-year measurements of fruit production of 250 individuals distributed on a 27-ha area of subalpine forest in the Western Carpathians (Poland). Population- and individual-level interannual variability of fruit production was moderate. Synchrony among individuals was relatively high for all years, but the trees were much less synchronized in heavy crop years than in years of low fruit production. Weak

synchrony among trees for heavy production years suggests that the predator satiation hypothesis does not explain the observed masting behavior. Fruit production, both at individual and at population level, was highly correlated with weather conditions. However, the presence of masting cannot be fully explained by the resource-matching hypothesis either. We suggest that adverse weather conditions effectively limit fruit production, causing high inter-individual synchrony in low crop years, whereas the unsynchronized heavy crop years seem to have been affected by individually available resources.

Keywords Endogenous cycles · Individual masting · Interannual variability · Predator satiation · Seed production

Introduction

Mast seeding is defined as intermittent highly variable production of seed crops by a plant population (Silvertown 1980; Kelly 1994; Koenig and Knops 2000). Although masting is a population phenomenon, it is in fact the result of the reproductive patterns of individuals. It involves three components: individual interannual variability, individual endogenous cycles of temporal autocorrelation and interplant synchrony (Koenig et al. 2003). Components of masting do not vary in parallel, and numerous combinations of

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individual variability and synchrony have been noted among plant species (e.g., Schauber et al. 2002; Koenig et al. 2003; LaMontagne and Boutin 2007).

There are several hypotheses explaining masting at population level. Mechanisms causing masting are related to specific patterns of seed production at individual level. The resource-matching (or weather tracking) hypothesis states that reproductive effort depends on favorable conditions affecting the plants' available resources. In this scenario, seed crops vary in response to environmental variation (Norton and Kelly 1988; Kelly 1994; Kelly and Sork 2002). Under weather tracking, relatively high synchrony among individuals arises incidentally as individuals experience similar weather, and the individual level of variability of seed production mirrors the variation of favorable conditions (Kelly and Sork 2002).

Another proximate mechanism of mast seeding is based on resource budget. Theoretical models say that masting can arise when a plant requires more resources to produce seeds than it is possible to acquire in 1 year, and therefore, produces seeds only in years when the energy reserve exceeds some threshold, regardless of favorable environmental conditions (Yamauchi 1996; Kelly and Sork 2002; Crone et al. 2009). The resource allocation mechanism leads to high individual variability and strong negative temporal autocorrelations of reproductive effort (endogenous cycle), although synchrony among individuals in a population is not required (Kelly and Sork 2002). However, only narrow range of environmental variation is needed to synchronize individuals (Crone et al. 2009).

From the evolutionary point of view, selection favoring occasional large reproductive efforts over regular smaller ones is needed for mast seeding to originate (economy of scale; Janzen 1978; Norton and Kelly 1988). Selection can separately act on individual interannual variability and inter-individual synchrony (Koenig et al. 2003). For many species, selective factors are the ultimate cause of masting, but weather and resources work as proximate causes. Thus, masting can be the result of a combination of proximate and ultimate causes as mechanisms of resource matching, resource allocation and selection are not exclusive and may act jointly (Kelly 1994; Kelly and Sork 2002).

To understand the proximate and ultimate mechanisms of mast seeding, we need to determine the role of individual interannual patterns and inter-individual synchrony (Herrera 1998b; Herrera et al. 1998;

Koenig et al. 2003). At population level, the interannual pattern of seed production may be the outcome of variability in the seed production of most seeding individuals. From studying individuals, we might determine whether the pattern of variability observed in a population is frequent among individuals. An individual-based study provides a platform for investigating how population seed production patterns can be influenced by individual features such as size or endogenous cycles (LaMontagne and Boutin 2007). Furthermore, only individual-oriented studies allow for analysis of synchrony among individuals (Crawley and Long 1995; Koenig et al. 1999; LaMontagne and Boutin 2007). In context of predator satiation hypothesis, it was found that the evolutionary interaction between masting and non-masting individuals is a frequency-dependent game in which masters reach the highest success when they constitute a large proportion of the population (Lalonde and Roitberg 1992). Studies considering individuals make possible the comparison of reproductive success among individuals displaying different level of synchrony in seed production with the general population.

In this study, we examine interannual variability, inter-individual synchrony and endogenous cycles in fruit production by *Sorbus aucuparia* L. (rowan) in a subalpine spruce forest. Our study is based on long-term observations of individual trees. Rowan is widely recognized as a masting species (Kobro et al. 2003; Satake and Bjørnstad 2004, 2008). Its masting is seen as an adaptive defense against seed predation (Kobro et al. 2003). Under selective pressure from predispersal seed predators, high interannual variability and high inter-individual synchrony can be expected in rowan populations (Silvertown 1980; Koenig et al. 2003). The interval between high crop years depends on the time needed for the predator population to starve and decline in number (Silvertown 1980). Concurrently, site productivity can influence the length of time required to recover after a heavy crop (Kelly and Sork 2002; Satake and Bjørnstad 2008). Rowan growing in subalpine spruce forest faces harsh climatic conditions, and seed production in rowan seems resource-limited (Pías and Gutáin 2006; Pías et al. 2007; Satake and Bjørnstad 2008), so intervals greater than 1 year between heavy crop years are expected. Weather and resources are always involved in mast seeding (Kelly and Sork 2002), but as yet no correlations or very weak correlations between

weather conditions and rowan seed crops have been found (Sperens 1997b; Wallenius 1999, Kobro et al. 2003). Nevertheless, because of harsh mountain weather conditions, we take into account their possible influence on the variability of rowan fruiting.

Specifically, this study examines (i) interannual variability of fruit production at individual and population levels, (ii) inter-individual synchrony of fruit production (addressing whether the level of synchrony among individuals changes with the distance between them and in mast and non-mast years), (iii) endogenous cycles of individual fruit production and population periodicity in heavy and low crop years and (iv) weather cues (temperature, precipitation) associated with variation of fruit production.

Methods

Study species

Sorbus aucuparia L. (Rosaceae, Maloideae) is a deciduous monoic fleshy-fruited tree. It lives 100–150 years and reaches 15–20 m in height (Kullman 1986). Flower buds develop in the year before anthesis (Sperens 1997b). Clusters of white hermaphroditic flowers are produced in late spring (May–June). The flowers are self-incompatible although not absolutely (Sperens 1996; Raspé et al. 2000; Pías and Gutáin 2006), and are pollinated by a wide range of insects (Pías and Gutáin 2006; Raspé et al. 2000). The fruits are subglobose pomes, ripe August–September (Raspé et al. 2000). The seeds are dispersed by animals, mainly birds and mammals (Raspé et al. 2000). The seeds frequently are predated by larvae of the microlepidopteran *Argyresthia conjugella* Zell., for which rowan is the principal host (Sperens 1997a; Kobro et al. 2003).

In Europe, rowan is one of the most common trees bearing fleshy fruits. In general, there are far fewer articles on endozoochorous fleshy-fruited trees than on economically important wind-dispersed dry-fruited trees (Herrera 1998a; Herrera et al. 1998), but because of numerous interactions of rowan with animals (pollination by insects, dispersal by frugivorous vertebrates and predispersal seed predation; Raspé et al. 2000) there are a number of reports on its seed production. High temporal variation in fruit production of rowan was reported by Wallenius (1999) and

Sperens (1997b). Satake and Bjørnstad (2008) described geographic variation of reproductive cycles of rowan across southern Norway. Predispersal losses of reproductive potential were assessed by Sperens (1997b) and Pías et al. (2007). Pías and Gutáin (2006) and Sperens (1996) found that fruit production is not pollen-limited. Several studies have concentrated on the relationship between variation of fruit production and dynamics of the specialized seed predator *Argyresthia conjugella* population, some of them reported the satiation mechanism in heavy crop years (Kobro et al. 2003; Satake et al. 2004; but see Sperens 1997a). Guitián and Munilla (2010) found that carnivores can be important dispersers of rowan seeds. However, there are still no long-term studies of seed production that consider interannual variability and synchrony among a large number of individuals of a local population.

Study site

The study was done in subalpine old-growth spruce forest on the Babia Góra massif (1,725 m a.s.l.) in the Western Carpathians (Poland). This forest has been under legal protection as a nature reserve since 1930.

Tree stands in the subalpine forest are built of *Picea abies* with sporadic occurrence of *S. aucuparia*. Small rowan thickets are a dynamic component of the forest and occur in gaps in spruce stands resulting from bark beetle outbreaks or windstorms (Żywiec 2008; Żywiec and Ledwoń 2008). The average density of rowan trees in an old-growth spruce forest is low, but rowans also form a persistent seedling and sapling bank (Holeksa and Żywiec 2005; Żywiec and Ledwoń 2008).

Data collection

We demarcated a 27-hectare (564 × 480 m) rectangular plot, representative for subalpine spruce forest, at 1,170–1,310 m a.s.l. on the north slope of the Babia Góra massif. All rowan trees in the plot with diameter at least 4 cm were mapped. The analysis used a group of 250 trees, i.e., all trees that bore fruits at least once in the studied period (2000–2010) and survived through 2010. Our intention was to study a local population consisting of individuals exposed to similar biocenotic, climatic and soil conditions. The whole plot is situated within one forest type and sandstone is the only

bedrock type. The 140-m altitudinal range rises the problem of variability in climatic conditions, which can influence the fruit production and its temporal variability. We included trees from the whole range after we had stated that fruit production and temporal synchrony among trees in fruit production do not change with increasing difference in altitude.

In 2000–2010, all trees were searched for fruits at the beginning of September before birds began to feed on them. Fruit production was measured by binocular observations, counting the number of infructescences (corymbs with fruits) on individual trees. It was possible to count infructescences with binoculars, because 75 % of trees were shorter than 10 m and only three of them were taller than 16 m, and ripe fruits were well visible against the background of green leaves. For each tree, five infructescences were randomly taken and all fruits in them were counted. In the first year of our study, only 27 % of trees had more than five infructescences. In next 4 years, fruit crop was also low and for most individuals we could not collect higher number of infructescences. Number of infructescences was considerably higher in heavy crop years. But, for comparisons among trees and years, the sample of five infructescences was accepted.

The fruit production of a tree was determined as the product of its number of infructescences and the average number of fruits in five infructescences. We used individual means of fruit number per infructescence, because we had found that intra-individual variability of fruit number in infructescences was lower than among individual variability and it was true both in low and high production years (ANOVA).

Data analysis

Variability of fruit production

To get the population-level coefficient of variation (CV_p), the fruit production of all 250 studied trees was summed for each year in 2000–2010. Then, CV_p was calculated as the ratio of the standard deviation of annual fruit production to long-term mean annual fruit production in 2000–2010. Similarly, the coefficient of variation of an individual tree (CV_i) was calculated using the standard deviation and the long-term mean of its fruit production in 2000–2010. Then, we calculated the mean CV_i of all trees (Herrera 1998b; Herrera et al. 1998).

It is usually difficult to classify mast versus non-mast years (Kelly 1994; Herrera et al. 1998). We decided to distinguish heavy crop years from low crop years, defining heavy crop years as years with fruit production higher than the long-term mean, and low crop years as those when fruit production was lower than the long-term mean. Those terms were used for both population- and individual-level fruit production.

Synchrony

To determine the level of synchrony of fruit production between trees during the 11 study years, the fruit production patterns of all pairs of individual trees were analyzed with Spearman's rank correlation. Mean inter-individual synchrony (r_s) was estimated as the mean of all pairwise Spearman's correlations between individuals. The 95 % confidence interval was calculated on the basis of 5,000 bootstrap resamples (Buonaccorsi et al. 2001; Koenig et al. 2003). We used Spearman's rank correlation as our data were not normally distributed (in 241 of 250 cases; Shapiro–Wilk test). Furthermore, in many trees, there were several zero values (no fruit production in particular years). For such data, nonparametric test is more adequate (see LaMontagne and Boutin 2007).

To find out whether synchrony between trees changes with distance, we used the Mantel test, which can assess the relationship between distance and correlation coefficients for pairs of trees (Poncet et al. 2009). Spearman's coefficients were used, and 5,000 randomization trials were performed. Distance between trees was measured in ArcGIS 9.1. (ESRI) software.

We also examined whether the level of synchrony among trees differed for heavy and low crop years. For each year, we calculated the proportions of trees that had fruit production above and below their 11-year mean. We posited that in heavy crop years, the higher the proportion of trees with fruit production above their 11-year means, the higher the level of synchrony among trees. Conversely, in years of low production, the higher the proportion of trees with fruit production below their 11-year means, the higher the level of synchrony.

Endogenous cycles

To test for the presence of endogenous cycles of fruiting within individuals, we calculated temporal autocorrelation functions (ACF). Successive lags of 1,

2 and 3 years were examined. No lags greater than 3 years were studied because of the short length of the series. Population-level ACFs were also calculated to search for any periodicity of variability in heavy and low crop years.

Influence of environmental conditions

Data on weather conditions for the study period came from the nearest meteorological station. The data were monthly minimum ground temperatures and monthly total precipitation. Spearman's correlation coefficients were used to assess the relationship between weather conditions and fruit production and frequency of fruiting trees in particular years.

Results

Variability

During 11 years, mean annual seed production varied strongly at the population level. The fruit crop ranged from 1 to 4,322 fruits/tree (on average 1,370 fruits/

tree; Fig. 1a). The interannual variability of fruit production at the population level was moderate ($CV_p = 1.07$). Much lower was the interannual variability of the frequency of fruiting trees ($CV = 0.42$) and in most years, the frequency was high (Fig. 1b). Population heavy crops were observed in 2005, 2006, 2007 and 2009 (Fig. 1a). Interannual variability of fruit production widely ranged among individuals (CV_i from 0.73 to 3.32; on average 1.62).

Synchrony

The level of synchrony of fruit production among trees was high (mean $r_s = 0.61$; bootstrapped 95 % confidence interval: 0.49–0.78). The synchrony among trees even slightly increased with increasing distance between trees, although the extremely low value of correlation coefficient (Mantel test, $r = 0.04$, $P < 0.0001$) suggests that the effect of distance on the synchrony within the studied range of distances can be neglected.

Individual temporal crop patterns considerably varied among trees. There was no consistent pattern shared by most trees. In the four population heavy crop

Fig. 1 **a** Individual fruit production of *Sorbus aucuparia* (mean \pm SE) and long-term mean fruit production at population level (dotted line) in 2000–2010. **b** Frequency of fruiting trees

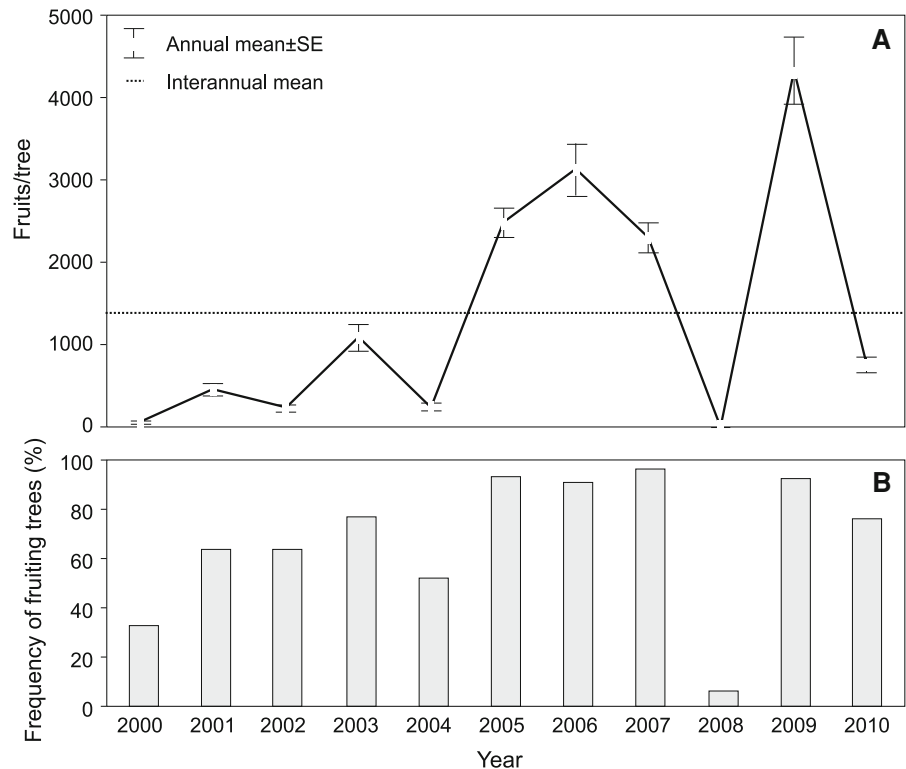


Table 1 Spearman's rank correlations between weather conditions in current and previous years (minimum monthly ground temperature and sum of monthly precipitation) and fruit production and frequency of *Sorbus aucuparia* fruiting trees

	Current year				Previous year			
	Min <i>T</i>		Precipitation		Min <i>T</i>		Precipitation	
	Pr.	Fr.	Pr.	Fr.	Pr.	Fr.	Pr.	Fr.
April	0.10	−0.11	−0.26	−0.39	0.24	0.20	−0.16	−0.01
May	0.15	−0.02	0.23	0.40	<i>0.82**</i>	<i>0.79**</i>	−0.15	−0.14
June	0.12	0.20	0.38	0.37	0.04	−0.01	−0.14	−0.15
July	0.26	0.19	<i>−0.81**</i>	<i>−0.84**</i>	0.33	0.23	−0.04	−0.09
August	0.38	0.20	0.47	0.42	0.56	<i>0.69*</i>	0.44	0.56
September	–	–	–	–	0.09	0.21	−0.24	−0.21
October	–	–	–	–	0.46	0.27	−0.61	−0.48

Values with a significant level of $P < 0.05$ are shown in italic type

Min *T* minimum monthly ground temperature, *Pr.* population fruit production, *Fr.* frequency of fruiting trees

* $P < 0.05$. ** $P < 0.01$

years, individual trees differed in the number of years they contributed to the population's heavy crop. The trees with individual heavy crops in all 4 years formed the largest group but they accounted for only 21 % of the trees. A similar fraction (18 %) had a heavy crop every other year—2005, 2007 and 2009. There were also three smaller but sizeable groups of trees, first of them had their heavy crops in 2005, 2006 and 2009 (12 %), second one in 2006 and 2007 (10 %) and third one in three consecutive years (2005–2007) but not in 2009 (9 %). In general, there were a number of different patterns of fruit production by individual trees, and no group clearly prevailed.

The trees were less synchronized in the heavy crop years than in the years of low fruit production. In years with population heavy crops, considerable parts of the trees (22.4–38.4 %; on average 29.3 %) still had crops lower than their individual interannual means. Whereas in population low crop years, only small parts of the trees (0.0–22.8 %; on average 7.4 %) showed fruit production higher than their individual means.

Endogenous cycles

We found no individual endogenous cycles in fruit production. Individual fruit production in a current year was independent on fruit production in previous 3 years and next 3 years. There was no temporal autocorrelation of fruit production for 243 out of 250 trees. The result was no interannual periodicity of fruit production at population level.

Influence of weather conditions

There were some relationships between rowan fruit production and the weather conditions in the current and previous years. At the population level, fruit production and the frequency of fruiting trees increased with decreasing precipitation in July of the same year, and increasing previous year's May minimum ground temperature (Table 1). Those two weather variables influenced individual fruit production patterns of majority of trees (75 and 72 %, respectively). Furthermore, the frequency of fruiting trees increased with increasing the previous year's August minimum ground temperature, but this relationship was not significant for population fruit production (Table 1). Individual interannual fruit production pattern was significantly correlated with this weather variable only for 42 % of trees.

Discussion

Variability

We found the moderate interannual variability of fruit production, which even fit within the range reported by Kelly et al. (2001) for plants that do not derive any selective benefits or disadvantages from mast seeding. It was rather unexpected result, as rowan experiences a high level of specialized seed predation (Sperens 1997a; Kobro et al. 2003). *A. conjugella* is a

predisersal seed predator that can cause substantial seed loss in rowan (Sperens 1997a; Kobro et al. 2003). In low crop years, it can destroy most seeds in this subalpine spruce forest (Żywiec, unpublished data). According to the predator satiation hypothesis, high interannual variability of seed crops limits the population density of predators by starving them in low crop years and satiating them in years of high seed production, allowing a portion of seeds to escape (Silvertown 1980). In southern Norway, this hypothesis was supported for rowan (Satake et al. 2004). On a local scale, however, Sperens (1997a) found that rowan seed predation did not reflect the operation of predator satiation.

In considering selection for masting, it is important to remember that rowan experiences selective pressure not only from predisersal seed predators but also from insects pollinating its flowers and from frugivorous vertebrates that disperse its seeds. In such a circumstance, fruit and seed production are under conflicting pressures: starvation and satiation of seed predators on one hand and avoidance of satiation and starvation of pollinators and dispersers on the other (Herrera et al. 1998). However, it seems that unspecialized frugivorous dispersers and pollinators of rowan do not select strongly against variability of fruit production (Sperens 1996; Pías and Gutáin 2006; Guitián and Munilla 2010). On the other side selection exerted by highly specialized seed predators should generate predator satiation mechanisms employing high interannual variation, high synchrony and intervals between heavy crop years.

Synchrony

The mean inter-individual synchrony of rowan fruit production was relatively high as compared with other species (Koenig et al. 2003). However, this inter-individual synchrony we found during 11-year observations seems to be mainly a result of low fruit production by most trees in years of population low crops. In population heavy crop years, a considerably smaller share of individuals had their heavy crops. This suggests that the recorded high inter-individual synchrony is mainly the effect of high synchrony in low production years, and it does not necessarily speak for simultaneous high seed production by most individuals, i.e., for mast years. We found that individuals showed several patterns of fruiting in heavy crop years. Only about 20 % contributed

appreciably in all 4 population heavy crop years. In the other trees, heavy crops occurred 1–3 times and no temporal pattern dominated.

Such a fruiting pattern has consequences for seed predation. High synchrony in low crop years can give an advantage at the population level by starving the seed predator. At an individual level, high synchrony also means that there are few unsynchronized trees, which could lose their crops and waste resources in low crop years. On the other side, weak synchronization among trees in heavy crop years can have serious negative consequences for reproduction. At population level, a lack of synchrony results in several consecutive years of heavy crops. Then, the seed predator population can expand considerably and destroy more and more seeds over time. At individual level, although low fruit production in favorable weather conditions should promote accumulation of resources for future reproduction, trees producing an abundance of fruits later in a series of population heavy crop years can lose more of them due to predation than trees producing a heavy crop right after synchronous low crop years.

Endogenous cycles

There was no periodicity of individual fruit production. For almost all individuals, fruit production in a given year was independent of production in the preceding 3 years. More than half of the rowan trees had above-mean fruit production in at least two consecutive years. This seems to negate the resource budget hypothesis that fruit production in a current year is limited by high fruit production in previous years. On the other hand, heavy crops in two or three consecutive years may be an effect of low fruit production by most individuals for first five study years in a row. Resources accumulated during this time might be sufficient for more than 1 year of heavy fruiting. For *Fraxinus excelsior* in Sweden, Tapper (1992) recorded a similar predisposition for high crops in two consecutive years.

The tendency to produce heavy crops in consecutive years was not consistent among trees. A considerable share of them (about 40 %) had heavy crops preceded and followed by at least 1 year of low crop. The lack of a significant autocorrelation for almost all individuals may be the result of several consecutive years of low fruit production at the beginning of the

study period, combined with the short duration of the study. Koenig et al. (2003) suggest that finding autocorrelations depends on the number of study years, especially for lags longer than a year. As studies examining endogenous cycles of individual trees require long-term data, they are very rare (but see LaMontagne and Boutin 2007).

As a consequence of the lack of periodicity of fruit production at the individual level, we did not find regularity of the intervals between low and high production years at population level either. There were 3 consecutive years of heavy crops after 5 years of more or less low fruit production, and then only 1 year of low production preceded an extremely heavy crop in 2009. Three heavy crop years in a row are unexpected in plants experiencing the selective pressure of a seed predator. Selective pressure of seed predators is expected to result in at least a 1-year gap between high production years, to reduce the seed predator population (Silvertown 1980). The observed lack of such an interval suggests that rowan in subalpine spruce forest is not well adapted to such pressure or the pressure of the seed predator is not effective enough. Although, periodicity in fruit production was found in this species in north of Europe (Wallenius 1999; Kobro et al. 2003; Satake and Bjørnstad 2008).

Influence of environmental conditions

Fruit production at the population level was highly correlated with the weather conditions of the current and previous years; both fruit production and the frequency of fruiting trees were highly correlated with them. Furthermore, at the individual level, we obtained these correlations for trees with the highest fruit production, that is, the trees that are decisive for the population's crop, as well as for most individuals with low fruit production. Those results are in contrast with previous studies of rowan, which found weather conditions (temperature and precipitation) to have no impact (Sperens 1997b; Wallenius 1999) or a very weak impact (Kobro et al. 2003) on the fruit crop.

The number of fruits produced was negatively affected by high precipitation in July of the same year. Rowans in subalpine spruce forest set fruits at the beginning of July, so the trees may be particularly sensitive to weather conditions at that time. There was a positive correlation between fruit production and

minimum ground temperature in May of the previous year. Temperatures during flower initiation influence seed production in a variety of species (Norton and Kelly 1988; Schaubert et al. 2002). Our results may suggest that temperature during the previous May influences rowan fruit production by affecting flower bud production. Low minimum ground temperature in August lowered the frequency of fruiting trees in the following year. This correlation was weaker than the previous two correlations. Nevertheless, such a relationship seems reasonable. Low August temperatures probably shorten the growing season, decreasing the amount of resources accumulated for reproduction the following year.

The fruit production of most individual trees was correlated with weather conditions, though we did find a variety of individual patterns of heavy crops. The high correlations mainly seem because of the strong effect of weather in preventing reproduction and causing synchronization among trees in low crop years. Sperens (1997b) demonstrated that even fertilization cannot increase rowan fruit production in unfavorable years. As low crop years were the majority of years in the studied period, high synchrony among individuals was our result even though we could find no dominating temporal pattern of heavy crop years among the trees.

The observed high correlation between weather conditions and the fruit crop suggests the resource-matching hypothesis as an explanation of the variability of rowan fruit production in subalpine spruce forest. At the heart of this hypothesis, however, is the idea that heavy crops occur in response to favorable weather conditions (Kelly and Sork 2002). In our study, individuals do not respond synchronously to favorable conditions, so the resource-matching hypothesis apparently does not explain all the variability of fruit crops. Because the resource-matching hypothesis assumes that in good years both growth and reproduction increase, evidence that resource allocation switches from vegetative growth to fruit production in high crop years would negate the resource-matching hypothesis and simultaneously demonstrate that variation of fruit production is the result of selection (Monks and Kelly 2006).

In conclusion, studying fruit production simultaneously at both levels—individual and population—gave us a better understanding of its conditions and consequences. Using trees as sampling units can

reveal the contribution of individuals to population variability. The specific temporal variability of the seed crop at population level may arise as an effect of many combinations of individual patterns and inter-individual synchrony. To verify a particular hypothesis about masting, the temporal variability of seed production at individual level needs to be taken into consideration. Our long-term study of a large sample of individuals made it possible for us to ascertain that the inter-annual changes in fruit production in that population could not be fully explained by any hypothesis of masting. Alone, neither resource-matching, resource allocation nor predator satiation mechanisms determined the fruit production pattern. We suggest that adverse weather conditions, common in the subalpine zone, effectively limit seeding, causing strong inter-individual synchrony in low crop years. Unsynchronized heavy crop years seem to be affected by the available resources and the endogenous cycles of individual plants.

Acknowledgments We are grateful to Prof. Jerzy Szwagrzyk for valuable suggestions during preparation of the manuscript. We thank also to Dr. Wojciech Bąba for his help in statistical analysis. This study was funded by the Polish State Committee for Scientific Research (grant no. 3P04G11125, 6 P04G 045 21 and N304 362938). The statutory fund of the Institute of Botany of the Polish Academy of Sciences also provided partial funding.

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