

Trees (2013) 27:1365–1373
DOI 10.1007/s00468-013-0884-y

ORIGINAL PAPER

Does a heavy fruit crop reduce the tree ring increment? Results from a 12-year study in a subalpine zone

Magdalena Żywiec · Tomasz Zielonka

Received: 3 December 2012 / Revised: 25 March 2013 / Accepted: 11 May 2013 / Published online: 24 May 2013
© The Author(s) 2013. This article is published with open access at Springerlink.com

Abstract Life history theory posits that an increased investment in reproduction should result in decreased vegetative investment. Switching resources from growth to reproduction are also expected in species experiencing selection pressure for high variation of seed crops. In this study, we tested whether the reproductive effort of trees, measured as the number of fruits produced, is related to their radial growth increment. We examined a population of *Sorbus aucuparia*, a fleshy-fruited tree species with highly variable interannual individual fruit production growing in the subalpine zone and under strong selection pressure from pre-dispersal seed predators. We used 12-year data to test the relationship between fruit crop and radial growth increments in current, previous and subsequent years, and found no trade-off between growth and reproduction. For almost all trees, there was no correlation between fruit crop and radial growth increment in the same year or next year. Only a few trees showed a positive correlation between fruit crop and previous-year growth. In the statistics, we took advantage of the high variability of individual fruit crops in high production years. In four heavy crop years, we compared the radial growth increments of trees with heavy crops with those of trees with low fruit crops. Current and next-year radial growth did not differ between trees with low and high fruit crops. In all

those years, however, trees having heavy fruit crops had higher previous-year growth increments. We suggest that the harsh subalpine weather conditions account for the lack of a trade-off between growth and reproduction in the studied population.

Keywords Cost of reproduction · Masting · Trade-off · Vegetative growth

Introduction

In explaining resource allocation patterns, life history theory assumes that the vegetative and reproductive functions of plants compete for a common limited pool of resources. An increased investment in reproduction is expected to result in decreased vegetative investment (trade-off hypothesis; Harper 1977; Reznick et al. 1986; Reekie and Bazzaz 1987; Obeso 2002). While the amount of resources invested in reproduction constitutes a direct cost of reproduction (reproductive allocation), the consequences of this investment for somatic functions constitute an indirect cost of reproduction (somatic cost of reproduction; Reekie and Bazzaz 1987; Kalson and Méndez 2005). Allocation of resources to current reproduction deprives vegetative growth of these resources and in consequence reduces plant size and resource storage. Reduced growth in turn leads to reduced future survival and future reproduction (Reekie and Avila-Sakar 2005).

The existence of somatic costs of reproduction is a basic plank of life history theory, but measuring such costs is difficult and not straightforward (Reznick 1985; Silvertown and Dodd 1999; Obeso 2002). There are numerous examples of a negative relationship between reproduction and growth in the same or next year (Eis et al. 1965; Tappeiner

Communicated by D. Treutter.

M. Żywiec (✉)
Institute of Botany, Polish Academy of Sciences,
ul. Lubicz 46, 31-512 Kraków, Poland
e-mail: m.zywiec@botany.pl

T. Zielonka
Institute of Biology, Pedagogical University of Cracow,
ul. Podchorążych 2, 30-084 Kraków, Poland

1969; Gross 1972; Koenig and Knops 1998; Nicotra 1999; Silvertown and Dodd 1999; Monks and Kelly 2006; Han et al. 2008; Ishihara and Kikuzawa 2009; Camarero et al. 2010; Drobyshev et al. 2010), but also examples of no relationship (Willson 1986; Cremer 1992; Yasumura et al. 2006; Knops et al. 2007) and even of a positive relationship (Reekie and Bazzaz 1987; Despland and Houle 1997).

The trade-off between vegetative growth and reproduction is an important assumption in the theory of masting behavior, that is, synchronous and highly variable annual seed production in a population of perennial plants (Kelly and Sork 2002). To demonstrate that masting behavior in a given population is a result of selection for temporally variable seed production rather than simply a response to weather conditions, Norton and Kelly (1988), Monks and Kelly (2006) suggested that the most important thing is to prove that switching operates i.e. that resources are diverted towards reproduction in some years and away from reproduction in other years. Switching should result in a negative relationship between resources devoted to reproduction and to growth (trade-off). Selection favors occasional large reproductive efforts over regular smaller ones when economies of scale operate, for example, when heavy crops satiate seed predators or increase the efficiency of wind pollination (Kelly 1994; Kelly and Sork 2002). An alternative explanation of variable seed production is the resource matching hypothesis (or weather tracking hypothesis): under variable weather conditions, the seed production pattern reflects this variation (Kelly and Sork 2002). In this case, Monks and Kelly (2006) suggest that in good years, plants should have both high reproduction and high vegetative growth. The trade-off mechanism would result in a negative correlation between growth and reproduction, and resource matching would produce a positive correlation.

In trees, the somatic cost of reproduction can be assessed from tree ring increments. Most long-term studies of tree seed production have been based on data from seed traps on a population, regional or even geographic scale (Norton and Kelly 1988; Koenig and Knops 1998; Drobyshev et al. 2010). Some studies have assessed fruit crops indirectly by dating rachises and cones (Despland and Houle 1997; Silvertown and Dodd 1999). There are only a few long-term studies that follow individual variation of seed production and relate it to individual radial growth (but see Eis et al. 1965; Monks and Kelly 2006; Knops et al. 2007).

Our aim was to determine if heavy fruit crops cause a decrease of growth in a tree species experiencing strong selective pressure on masting strategy. To do this, we used 12-year data on the individual fruit crop and radial growth of 36 trees, in this case the fleshy-fruited *Sorbus aucuparia*, a species characterized by highly variable interannual

individual fruit production. The studied population grows under high selection pressure from pre-dispersal seed predators, and individuals with higher variation of fruit production experience lower seed predation (Żywiec et al. 2012, 2013). According to Monks and Kelly's (2006) predictions, we should expect a negative relationship between resources devoted to reproduction and to growth. The studied trees grow in the subalpine zone under harsh mountain weather conditions and a short growing season. In such circumstances, resources are strongly limited and a trade-off between growth and reproduction can be expected (Reznick 1985). In the studied population, the fruit crop is highly influenced by weather conditions, but the high correlation of fruit production with weather variables seems due mainly to the strong effect of weather in preventing reproduction and causing synchronization among trees in low crop years (Żywiec et al. 2012). Those trees were much more synchronized in years of low fruit production than in heavy crop years; in consequence, we found a variety of individual patterns of high crops. This makes the population eminently suitable for testing the influence of reproductive effort on the radial growth increment. In most years, we were able to compare the tree ring increments of individuals having high and low crops. As both groups experienced the same weather conditions, that influence on radial growth could be disregarded.

Materials and methods

Study species

Sorbus aucuparia L. (Rosaceae, Maloideae) is a deciduous fleshy-fruited tree. It lives 100–150 years and reaches 15–20 m in height (Kullman 1986; Hofgaard 1993). Flower buds develop in the year before anthesis (Sperens 1997). Clusters of hermaphroditic flowers are produced in late spring (May–June). The flowers are self-incompatible although not absolutely so (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 in August–September (Raspé et al. 2000). On average, the fruits are 9 mm in diameter, with fresh weight of 0.45 g and dry weight of 114 mg (Herrera 1987; Raspé et al. 2000). Flesh accounts for 50.1 % of the dry matter, skin 32.2 %, and seeds 17.7 %. The flesh is rich in sugars (17.7 % of dry matter) and ash (10.2 %), and the seeds contain crude protein (25.5 %), crude fat (16.5 %) and sugars (5.5 %) (Pulliainen 1978).

Rowan's climatic and edaphic requirements are low (Kullman 1986; Raspé et al. 2000). It is distributed through 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 2,000 m a.s.l. (Raspé et al. 2000). It is well adapted to the stress of winter desiccation and a short growing season, and can maintain a tree growth-form well above the natural treeline of most other species (Barclay and Crawford 1982; Kullman 1986). Hillebrand and Rosenberg (1996) found that at high altitude it shows less interannual radial growth oscillation than *Fagus sylvatica* and *Picea abies*.

Rowan is reported as having considerable interannual variation of individual fruit production. In previous work, we analysed the studied population's fruit production pattern in 2000–2010. The fruit crop ranged from 1 to 4,322 fruits/tree (avg. 1,370 fruits/tree). Interannual variability of fruit production varied widely between individuals (CV_i ; 0.73–3.32, avg. 1.62). The coefficient of variation of fruit production for the population (CV_p) was 1.07 (Żywiec et al. 2012). The fruit production pattern was strongly influenced by weather conditions, but the rowans responded synchronously only to unfavorable weather conditions; in good years, the fruit production of individual trees varied considerably. We found no endogenous cycles of individual fruit production. The conclusion was that rowan trees represent a large range of fruit production patterns (Żywiec et al. 2012). As it experiences strong pre-dispersal seed predation by *Argyresthia conjugella*, masting in this species has been suggested to be an adaptive defence against seed predation (Kobro et al. 2003; Satake et al. 2004). In the studied population, the intensity of pre-dispersal seed predation in 2005–2011 was high (range 19–100 %, avg. 70 %). There were both functional and quantitative responses of predators to the variation of fruit production at population level. Individuals expected to be preferred under seed predator pressure had higher reproductive success. The percentage of infested fruits decreased with increasing synchrony of fruit production between individual trees and the population. There was also a negative relationship between the interannual variation of individual fruit production and the percentage of infested fruits (Żywiec et al. 2013).

Study site

The study was done in a subalpine old-growth spruce forest on the north slope of the Babia Góra massif (1,725 m a.s.l.) in the Western Carpathians (Poland) at 1,170–1,310 m a.s.l. Tree stands in the studied forest are composed of *Picea abies* with sporadic occurrence of *S. aucuparia*. Small rowan thickets are a dynamic component of the forest, occupying gaps in spruce stands resulting from bark beetle outbreaks or windstorms (Holeksa et al. 2008;

Żywiec and Ledwoń 2008). The average density of rowans with dbh >7 cm is only about 31 trees per hectare (Holeksa et al. 2008), but rowans also form a persistent seedling and sapling bank in subalpine spruce forest (Holeksa and Żywiec 2005; Żywiec and Holeksa 2012).

In the subalpine forest belt, the climate is cool with 3.3 °C mean annual temperature, 1,470 mm mean annual rainfall, and a snow-free period of 7 months (Obrębska-Starkłowa 2004). The soils are mainly humus-iron podzols, iron podzols and podzolized rankers which developed from sandstone with mudstone interbedding (Miechówka et al. 2004).

Data collection

In 2000–2011, the rowan fruit crop was studied in a 27 ha permanent study plot in subalpine old-growth spruce forest on the north slope of Babia Góra (see Żywiec et al. 2012). All trees were searched for fruits at the beginning of September before birds began to feed on them. The fruit crop was measured by counting the number of infructescences (corymbs with fruits) on individual trees, using binoculars. Then five infructescences were taken randomly from each tree and all the fruits in them were counted. The fruit crop of a tree was determined as the product of the number of infructescences and the average number of fruits in the five collected infructescences (see Żywiec et al. 2012).

We chose 36 trees for radial growth increment analysis. The cored trees had similar dbh (mean 17 cm; range 10–29 cm) and were selected for their high mean interannual fruit production. All of them grew in approximately similar light conditions in small gaps. We have chosen trees with high mean interannual fruit production although stronger trade-offs can be expected in trees with low mean interannual fruit production (Sánchez-Humanes et al. 2011; Barringer et al. 2013). However, our study did not concentrate on finding if there is any relationship between growth and reproduction, but if individuals representing masting strategy (heavy fruit crops) show cost of this strategy in the vegetative growth. Thus, we tested the “switching” effect proposed by Norton and Kelly (1988), Monks and Kelly (2006). In the early spring of 2012, before the start of growth, the selected trees were cored with an increment borer (diam. 5 mm) along two radii at about 1 m above the tree base. The cores were mounted on wood slats, dried and progressively polished with a belt sander (up to grit 600) to make the tree ring sequences clearly visible. The samples were scanned (resolution 1,200 dpi). WinDendro software was used to measure the annual rings to 0.001 mm accuracy. We used visual cross-dating to precisely date each sample (Yamaguchi 1991).

The quality of the measurements was checked with COFECHA (Holmes 1983). Doubtful series were excluded from the dataset. If both series from one tree were acceptable, the mean of two radii was used as the measure of the radial growth increment in an individual tree. Otherwise, we took only the one acceptable series for further analysis.

Data analysis

We used three methods to find any relationship between the fruit crop and radial growth increment in the current, previous and subsequent year. At individual level, we used Spearman rank correlations to test whether the individual fruit production pattern was correlated with the sequence of radial growth increments (with lag -1 , lag 0 and lag $+1$).

In four heavy fruit crop years (2005, 2006, 2007, 2009), we tested whether the radial growth increments differed between groups of trees with high and low fruit crops. By this we meant to test the “switching effect” proponent by Kelly and the others (Norton and Kelly 1988; Monks and Kelly 2006). They suggest that that resources are diverted towards reproduction in heavy crop years and away from reproduction in low crop years in plants which experience strong selection pressure towards masting strategy. If masting strategy is an effect of evolution, the “switching” should be present in heavy crop years.

In these 4 years the between-tree variability of fruit crops was considerable; in each year, we could distinguish groups of trees with fruit crops higher and lower than their average individual fruit crop. First, the fruit production data were standardized; although we selected trees with relatively high mean fruit production, they still differed in their mean fruit crops. Data were standardized using means and standard deviations for 2000–2011. After standardization, the trees were ranged according to their standardized fruit crop. Then we selected the ten trees with the heaviest and the ten with the lowest standardized fruit crop. This was done separately for each of the 4 years. Then we used the Mann–Whitney test to compare the radial growth increments of the groups with high and low fruit crops in a particular year (with lag -1 , lag 0 and lag $+1$). The radial growth increments were compared for both—standardized and the raw data.

At population level, we used Spearman rank correlations to test whether the mean standardized fruit crops were related to the mean standardized radial growth increments (with lag -1 , lag 0 and lag $+1$).

We took other measures to exclude some factors that could influence the relationship between growth and reproduction. To rule out the possibility that the differences in fruit crop between groups were a consequence of

differences in diameter, in each of the 4 years (2005, 2006, 2007, 2009) we tested for differences in diameter between groups and found no such differences in any year (Mann–Whitney test; $p > 0.05$). We also checked whether there was any consistency of membership of the high and low fruit crop groups over the 4 years. Of the 36 studied trees, 23 (64 %) were in both the high and low fruit crop groups at least once in 2005, 2006, 2007 and 2009; 8 trees were only in the high fruit crop group, and 5 trees were only in the low fruit crop group. Thus, the two groups contained different trees each year.

Results

At population level, fruit production was not correlated with the radial growth increment of the same year. Mean standardized fruit production was not correlated with the mean standardized radial growth increment of the same year (Spearman rank correlation: $r = 0.27$; $p = 0.39$). In three of the four high production years recorded in the population (2005, 2006, 2007, 2009), the mean radial growth increments were above the long-term mean (Fig. 1). In years with mean standardized fruit productions below the long-term mean, mean standardized radial growth increments were also below the long-term mean growth increment in seven out of eight years (Fig. 1).

In none of the four high crop years did the two groups of trees (high and low fruit crop) differ in the raw radial growth increment and standardized radial growth increment of the same year (Mann–Whitney test; Table 1; Fig. 2).

In none of the 4 years following heavy crops did the standardized radial growth increment of the two production groups differ (Mann–Whitney test; Fig. 2). The raw radial growth increments were lower in the high crop group only in the year following 2007, and not after the other high crop years (Mann–Whitney test; Table 1).

In each year preceding a heavy crop year, the standardized radial growth increment was significantly higher in the high than in the low crop group (Mann–Whitney test; Fig. 2). There were no such differences in raw radial growth increments (Mann–Whitney test; Table 1).

For 2 of the 36 trees, individual fruit production was significantly and negatively correlated with the current radial growth increment. The correlation of fruit crop with the next-year radial growth increment was significantly negative for 1 tree and significantly positive for 1 tree. Seven trees showed a significant positive correlation between fruit crop and the previous-year radial growth increment (Spearman rank correlation; $p < 0.05$ in all cases).

Fig. 1 Individual standardized fruit crop (mean ± SE) and individual standardized radial growth increment (mean ± SE) in 2000–2011. Data for individuals were standardized using 12-year means and SD for each tree

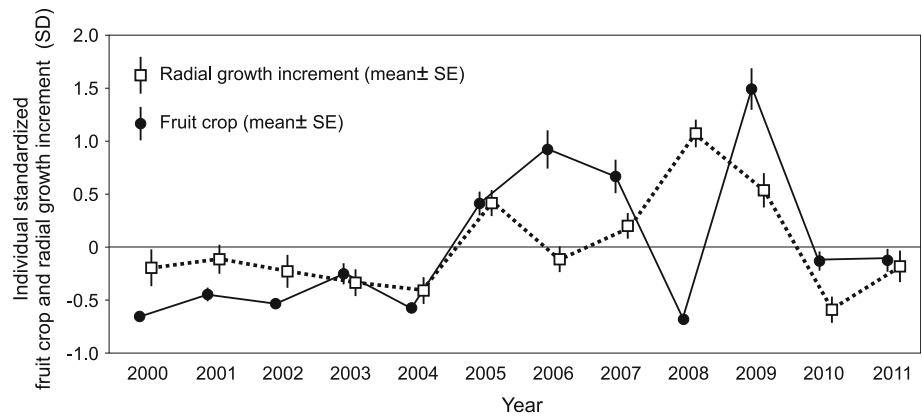


Table 1 Mean radial growth increments in years of high fruit crops (*t*), years before high fruit crops (*t*−1) and years after high fruit crops (*t*+1) in two groups of trees—those with high and low fruit crops in year *t*

Year <i>t</i>	Radial growth increment (mean) (mm)					
	Year <i>t</i>		Year <i>t</i> −1		Year <i>t</i> +1	
	High crop	Low crop	High crop	Low crop	High crop	Low crop
2005	1.313	1.314	1.338	0.959	1.110	1.292
2006	1.371	1.258	1.490	1.296	1.324	1.567
2007	0.941	1.650	0.968	1.322	1.155	2.089*
2009	1.687	1.054	2.055	1.116	0.873	0.845

Significant differences (Mann–Whitney test, *p* < 0.05) are *asterisked*

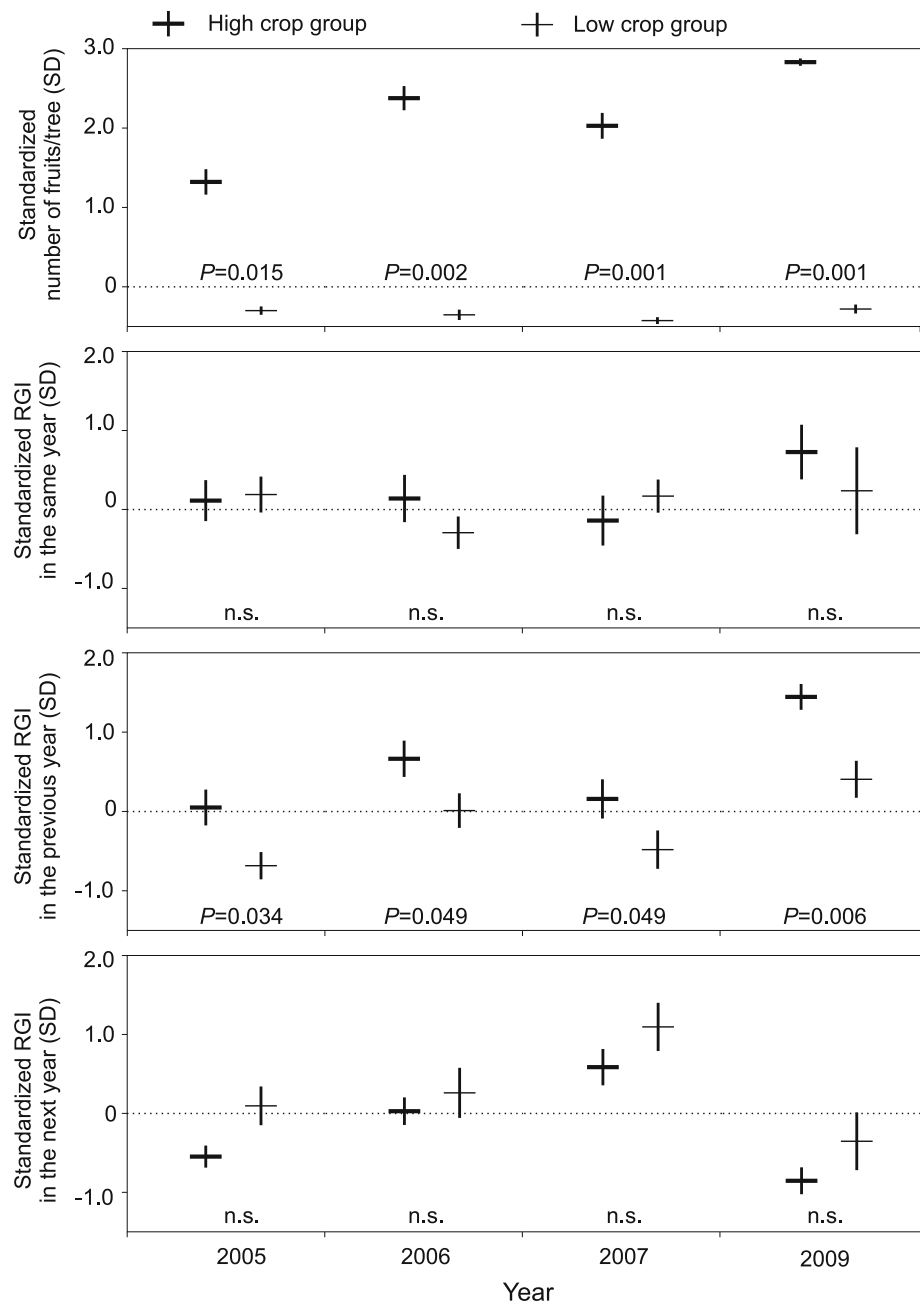
Discussion

In the studied rowan population, we found no trade-off between growth and reproduction. Almost all the trees showed no correlation between the fruit crop and the same-year radial growth increment. These results did not confirm the switching hypothesis. Our result is in line with results from southern Norway, where flowering of rowan also was not correlated with radial growth (Kobro et al. 2003). The lack of correlation between the individual fruit crop and tree ring growth might be explained by the fact that growth and reproduction are independently influenced by the same environmental variables, such as weather conditions (Knops et al. 2007). In our study, however, we found no trade-off between growth and reproduction when we controlled for the weather factor by taking into account individuals with high and low crops in the same heavy crop year, that is, in the same weather conditions. Sánchez-Humanes et al. (2011) suggest that the evidence for trade-offs is most likely to be found during a mast year in trees with large and small crops because the cost of reproduction may vary at this time among individuals with different levels of investment in acorn production. There was no difference in radial growth between the groups of trees with high and low fruit crops in

any of the population’s four heavy crop years. Thus, we can state that a heavy fruit crop did not limit the rowans’ current radial growth. Moreover, our results did not support resource matching as an explanation of the trees’ reproductive pattern. The group of trees with a higher fruit crop did not have thicker ring increments in any of the population’s heavy crop years, and none of the trees showed a positive relationship between growth and reproduction individually. However, the mean data for the population show that the radial growth increments were above the long-term mean in three of the four high production years. This suggests that some conditions good for growth also favored reproduction at the population level.

The lack of a trade-off between growth and reproduction seems surprising in a species under strong selection pressure from seed predators for high variation of fruit crops (Żywiec et al. 2013). There are several reasons why a trade-off may not be detected (Obeso 2002). One is selection against individuals that bear high costs of reproduction. Several mechanisms of compensation are known in plants (Reekie and Bazzaz 1987). Reproductive structures can photosynthesize, and indeed rowan fruits are green before ripening. Also, induction of reproduction can stimulate resource uptake in vegetative organs. Those mechanisms have their limits, however, and at high levels of reproduction they cannot compensate reproductive costs (Reekie and Avila-Sakar 2005). Yasumura et al. (2006) suggested that the radial growth increment is limited only when seed production exceeds a certain level. In our study, in 2009, the year of the heaviest fruit production observed in 12 years, there were no signs of a decreased ring increment in the group of trees with a high fruit crop. Another reason for the lack of a visible trade-off at the tree-stem level could be the modular nature of trees; branches and shoots can be quite autonomous in their resource budget and in consequence costs vary at the different canopy levels (tree canopy, branch, and shoot; Obeso 1997; Hoch 2005; Sánchez-Humanes et al. 2011). In *Styrax obassia*, Miyazaki et al. (2002) showed that reproductive

Fig. 2 Standardized number of fruits per tree and standardized radial growth increment (RGI) in the same, previous and next year, in groups of trees with high and low fruit crops in 2005, 2006, 2007 and 2009. Significant differences (Mann–Whitney test) are marked



shoots can bear most of the reproductive cost and that the main trunk allocates little storage starch to reproductive organs. In the context of cost of reproduction there is also an important mechanism of fruit abortion. Cost of fruit initiation can be higher than cost of increasing its size (Obeso 2002). If studied trees differed in level of fruit abortion it could influence observed relationship between growth and reproduction, as reproductive effort was measured as amount of ripe fruits produced. Another reason could be the fact that we chose only trees with high mean interannual fruit production for this study. Sánchez-Humanez et al. (2011) found that costs of reproduction are not

universal in a population of *Quercus lobata* and these costs may vary among trees with high production versus trees of low seed production and the resources to produce seeds seem more limited in the low-producing trees than in the high producers. Another confounding factor could be the variability of the local conditions. Barringer et al. (2013) suggested that when local environments are highly variable, trade-offs between traits might differ among sites and/or among years.

Our results showed that fruit-heavy rowan trees have enough resources to support both biomass accumulation and high fruit production. In a long-term study of five oak

species showing large interannual variability of seed crops, Knops et al. (2007) demonstrated that growth and reproduction can be largely or entirely independent of each other. Instead, they found a trade-off between current and future reproduction, and that the seed crop depends strongly on weather conditions. Weather and resources are always involved in mast seeding, and the amount of resources that can be allocated to reproduction depends on assimilation rates, which are affected by weather conditions (Kelly and Sork 2002). Weather is often a synchronizing cue of masting behavior; unfavorable weather can prevent reproduction. This last condition seems especially important in our subalpine rowan population. In earlier work, we found a variety of individual patterns of high crops but the fruit production of most trees was correlated with weather conditions; the strong effect of weather in preventing reproduction caused synchronization among trees in low crop years (Żywiec et al. 2012). Sperens (1997) demonstrated that even fertilization cannot increase rowan fruit production in unfavorable years.

We suggest that the harsh mountain weather conditions account for the lack of a trade-off between growth and reproduction in this subalpine rowan population. Monks and Kelly (2006) suggested that selection pressure from seed predators should lead to a trade-off between growth and reproduction. Seed predators do exert strong selection pressure in our rowan population (Żywiec et al. 2013). Such selection can lead to high interannual variability of seed production (Silvertown 1980). But in this population, it is possible that the severe weather conditions outbalance seed predator selection in their effect on fruit crop variability. Most likely the weather is the dominant factor determining the fruit production pattern, leading to high variation of fruit crops; selection from seed predation influences that variation to a lesser degree. This is in line with the suggestion that restrictive climatic conditions select against individuals expressing reproductive cost. Moreover, in high altitudes cost of reproduction can be minimized, especially in long-lived plants, as a result of weather anomalies which often cause reproductive failure. The saved resources may contribute to reducing reproductive cost in years of fruit production (Hemborg 1998; Hemborg and Karlsson 1998; Obeso 2002).

The relationship between growth and reproduction depends strongly on resource availability. In the subalpine zone, the resources seem to be strongly limited as a consequence of the mountain climate (Żywiec et al. 2012). Monks and Kelly (2006) predicted that plant species should show resource matching under highly variable, unfavorable environments where both reproduction and growth are possible only in good years. Indeed, growth and reproduction correlate positively in some species growing in

harsh conditions (Despland and Houle 1997). We did not find positive relationship between the fruit crop and the same-year radial growth increment. In three high crop years (2005, 2007, 2009), the mean ring growth was above the long-term mean, but it was below the long-term mean in one high production year. Part of our results may suggest that conditions good for growth were also good for reproduction, but they were not consistent between years. Some weather conditions influence both growth and reproduction; others can be limiting to only one of them. In some cases, a given condition influences growth and reproduction in opposite ways, and then the correlation between growth and reproduction can be negative even without a trade-off (Knops et al. 2007). Fruit production seems to respond to weather and climate episodes more than radial growth does. Disruption of one of the stages—flowering, pollination or fruit formation—can drastically reduce the crop (Kelly and Sork 2002). The same bad weather episodes may not influence wood production at all, or the loss of new cell formation may be compensated during the growth season. Simultaneously, it is important to remember that weather is not the only condition that affects rowan growth and reproduction; plant diseases and insects can as well (Raspé et al. 2000).

In this study, trees with a high fruit crop had higher previous-year radial growth increments. There are at least two possible explanations for that result. The first is related to the fact that rowan flower buds develop the year before fruiting (Sperens 1997). That is when the potential number of flowers is determined. Conditions advantageous for tree ring growth may very well be conducive to flower bud formation. Silvertown and Dodd (1999) found the same positive association between previous ring increment and seed production in *Abies balsamea* growing in subalpine forest, and Drobyshev et al. (2010) reported such a finding in *Fagus sylvatica* in southern Sweden. Drobyshev et al. (2010) suggested that better growth conditions can also promote primordium differentiation. The second explanation assumes that rowan trees have a large fruit crop when they accumulate a sufficient amount of resources. It has often been asserted that mast species must store resources in more than 1 year to produce large crops (Sork et al. 1993; Koenig et al. 1994; Satake and Iwasa 2000). If the conditions favoring tree ring growth are also good for resource storage, trees with a higher growth increment will have more reserves and yield a bigger fruit crop the next year. The data from this study do not say whether the higher fruit crops resulted from a greater number of flower buds or from higher resource storage. The latter seems less probable, though, as it would conflict with previous results on the fruiting pattern in that population. There were no endogenous cycles of individual fruiting; moreover, more

than half of the rowan trees had above-mean fruit production in at least two consecutive years, and 30 % of them had three consecutive years of heavy fruiting (Żywiec et al. 2012). This is in opposition with the hypothesis that rowans gain resources for heavy fruit crop for more than 1 year. Weather conditions in the previous year seem important for the seed crop, as recorded in several species including rowan (Piovesan and Adams 2001; Schaubert et al. 2002; Żywiec et al. 2012). In most cases, however, specific mechanisms shaping this relationship have not been found.

We observed no switching in the studied population even though it is under strong pressure from seed predators. We suggest that severe weather conditions affect the reproductive pattern of rowan more than pressure from seed predators does. While we did not detect a switching mechanism, we did find some relationship between reproduction and growth. The trees with the heaviest fruit crops were the ones with the largest previous-year radial growth increment. As also suggested by Reekie and Avila-Sakar (2005), to understand factors determining the somatic cost of reproduction, we need to know which factors determine vegetative growth in particular environmental conditions.

Acknowledgments We thank the authorities and staff of Babia Góra National Park for their kind cooperation and for granting permission to conduct this study. Michael Jacobs finally edited the manuscript. This study was funded by the Polish State Committee for Scientific Research (grant nos. 6 P04G 045 21 and 3 P04G 111 25), the Polish Ministry of Science and Higher Education (N304 362938), and the statutory fund of the Institute of Botany of the Polish Academy of Sciences. The methodology complies with the current laws of Poland in which the experiments were performed.

Open Access This article is distributed under the terms of the Creative Commons Attribution License which permits any use, distribution, and reproduction in any medium, provided the original author(s) and the source are credited.

References

- Barclay AM, Crawford RM (1982) Winter desiccation Stress and resting bud viability in relation to high altitude survival in *Sorbus aucuparia* L. *Flora* 172:21–34
- Barringer BC, Koenig WD, Knops JMH (2013) Interrelationships among life-history traits in three California oaks. *Oecologia* 171:129–139
- Camarero JJ, Albuixech J, López-Lozano R, Auxiliadora Casterad M, Montserrat-Martí M (2010) An increase in canopy cover leads to masting in *Quercus ilex*. *Trees* 24:909–918
- Cremer KW (1992) Relations between reproductive growth and vegetative growth of *Pinus radiata*. *For Ecol Manage* 52:179–199
- Despland E, Houle G (1997) Climate influences on growth and reproduction of *Pinus banksiana* (Pinaceae) at the limit of the species distribution in eastern North America. *Am J Bot* 84:928–937
- Drobyshev I, Övergaard R, Saygin I, Niklasson M, Hickler T, Karlsson M, Sykes MT (2010) Masting behaviour and dendrochronology of European beech (*Fagus sylvatica* L.) in southern Sweden. *For Ecol Manage* 259:2160–2171
- Eis S, Garman EH, Ebell LF (1965) Relation between cone production and diameter increment of Douglas Fir (*Abies grandis* (Dougl.) Lindl.) and Western White Pine (*Pinus monticola* Dougl.). *Can J Bot* 43:1553–1559
- Gross HL (1972) Crown deterioration and reduced growth associated with excessive seed production by birch. *Can J Bot* 50:2431–2437
- Han Q, Kabeya D, Iio A, Kakubari Y (2008) Masting in *Fagus crenata* and its influence on the nitrogen content and dry mass of winter buds. *Tree Physiol* 28:1269–1276
- Harper JL (1977) Population biology of plants. Academic Press, London
- Hemborg AM (1998) Cost of reproduction in subarctic *Ranunculus acris*: a five-year field experiment. *Oikos* 83:273–282
- Hemborg AM, Karlsson PS (1998) Altitudinal variation in size effects on plant reproductive effort and somatic costs of reproduction. *Ecoscience* 5:517–525
- Herrera CM (1987) Vertebrate-dispersed plants of the Iberian Peninsula: a study of fruit characteristics. *Ecol Monogr* 57:305–331
- Hillebrand K, Rosenberg A (1996) Investigations of growth and ecotypes of rowan, *Sorbus aucuparia*. *Forst Holtz* 51:216–220
- Hoch G (2005) Fruit-bearing branchlets are carbon autonomous in mature broad-leaved temperate forest trees. *Plant Cell Environ* 28:651–659
- Hofgaard A (1993) Structure and regeneration patterns in a virgin *Picea abies* forest in northern Sweden. *J Veg Sci* 4:601–608
- Holeksa J, Żywiec M (2005) Spatial pattern of a pioneer tree seedling bank in old-growth European subalpine spruce forest. *Ekologia* 24(3):263–276
- Holeksa J, Żywiec M, Parusel J, Szewczyk J, Zielonka T (2008) Subalpine spruce forests in the Babia Góra National Park. In: Saniga M, Kucbel S, Holeksa J, Żywiec M, Parusel J, Szewczyk J, Zielonka T, Jaworski A, Kołodziej Z, Bartkiewicz L (eds) Structure, production, coarse woody debris and regeneration processes of Norway spruce natural forest in National Nature Reserves Babia hora and Piłsko. Technical University in Zwolen, Faculty of Forestry, Zwolen, pp 49–96
- Holmes RL (1983) Computer assisted quality control in tree-ring dating and measurement. *Tree Ring Bull* 43:67–78
- Ishihara MI, Kikuzawa K (2009) Annual and spatial variation in shoot demography associated with masting in *Betula grossa*: comparison between mature trees and saplings. *Ann Bot* 104:1195–1205
- Kalson PS, Méndez M (2005) The resource economy of plant reproduction. In: Reekie EG, Bazzaz FA (eds) Reproductive allocation in plants. Elsevier Academic Press, Amsterdam, pp 1–49
- Kelly D (1994) The evolutionary ecology of mast seeding. *TREE* 9:465–470
- Kelly D, Sork VL (2002) Mast seeding in perennial plants: why, how, where? *Annu Rev Ecol Syst* 33:427–447
- Knops JMH, Koenig WD, Carmen WJ (2007) Negative correlation does not imply a tradeoff between growth and reproduction in California oaks. *PNAS* 104:16982–16985
- Kobro S, Søreide L, Djørnne E, Rafoss T, Jaastad G, Witzgall P (2003) Masting of rowan *Sorbus aucuparia* L. and consequences for the apple fruit moth *Argyresthia conjugella* Zeller. *Popul Ecol* 45:25–30
- Koenig WD, Knops JMH (1998) Scale of mast-seeding and tree-ring growth. *Nature* 396:225–226
- Koenig WD, Mumme RL, Carmen WJ, Stanback MT (1994) Acorn production by Oaks in central coastal California—variation within and among years. *Ecology* 75:99–109
- Kullman L (1986) Temporal and spatial aspects of subalpine populations of *Sorbus aucuparia* in Sweden. *Ann Bot Fen* 23:267–275

- Miechówka A, Niemyska-Lukaszczuk J, Zaleski T, Mazurek R (2004) Soils of the Babiogórski National Park. In: Wołoszyn B, Jaworski A, Szwagrzyk J (eds) The nature of the Babiogórski National Park. Monograph. Komitet Ochrony Przyrody PAN, Babiogórski Park Narodowy, Kraków, pp 197–211
- Miyazaki Y, Hiura T, Kato E, Funada R (2002) Allocation of resources to reproduction in *Styrax obassia* in a masting year. *Ann Bot* 89:767–772
- Monks A, Kelly D (2006) Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae). *Aust Ecol* 31:366–375
- Nicotra AB (1999) Reproductive allocation and the long-term costs of reproduction in *Siparuna grandiflora*, a dioecious neo-tropical shrub. *J Ecol* 87:138–149
- Norton D, Kelly D (1988) Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. *Funct Ecol* 2:399–408
- Obeso JR (1997) Costs of reproduction in *Ilex aquifolium*: effects at tree, branch and leaf levels. *J Ecol* 85:159–166
- Obeso JR (2002) The costs of reproduction in plants. *New Phytol* 155:321–348
- Obrębska-Starkłowa B (2004): Climate of the Babia Góra massif. In: Wołoszyn B, Jaworski A, Szwagrzyk J (eds) The nature of the Babiogórski National Park. Monograph. Komitet Ochrony Przyrody PAN, Babiogórski Park Narodowy, Kraków, pp 137–151
- Pías B, Gutáin P (2006) Breeding system and pollen limitation in the masting tree *Sorbus aucuparia* L. (Rosaceae) in the NW Iberian Peninsula. *Acta Oecol* 29:97–103
- Piovesan G, Adams JM (2001) Masting behaviour in beech: linking reproduction and climatic variation. *Can J Bot* 79:1039–1047
- Pulliamin E (1978) The nutritive value of rowan-berries, *Sorbus aucuparia* L., for birds and mammals. *Aquilo Ser Zool* 18:28–32
- Raspé O, Findlay C, Jacquemart A-L (2000) *Sorbus aucuparia* L. *J Ecol* 88:910–930
- Reekie EG, Avila-Sakar (2005) The shape of a trade-off function between reproduction and growth. In: Reekie EG, Bazzaz FA (eds) Reproductive allocation in plants. Elsevier Academic Press, Amsterdam, pp 189–214
- Reekie EG, Bazzaz FA (1987) Reproductive effort in plants. 3. Effect of reproduction on vegetative activity. *Am Nat* 129:907–919
- Reznick DN (1985) Costs of reproduction—an evaluation of the empirical evidence. *Oikos* 44:257–267
- Reznick DN, Perry E, Travis J (1986) Measuring the cost of reproduction: a comment on papers by Bell. *Evolution* 40:1338–1344
- Sánchez-Humanes B, Sork VL, Espelta JM (2011) Trade-offs between vegetative growth and acorn production in *Quercus lobata* during a mast year: the relevance of crop size and hierarchical level within the canopy. *Oecologia* 166:101–110
- Satake A, Iwasa Y (2000) Pollen coupling of forest trees: forming synchronized and periodic reproduction out of Chaos. *J Theor Biol* 203:63–84
- Satake A, Björnstad ON, Kobro S (2004) Masting and trophic cascades: interplay between rowan trees, apple fruit moth, and their parasitoid in southern Norway. *Oikos* 104:540–550
- Schauber EM, Kelly D, Turchin P, Simon C, Lee WG, Allen RB, Payton IJ, Wilson PR, Cowan PE, Brockie RE (2002) Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. *Ecology* 83:1214–1225
- Silvertown JN (1980) The evolutionary ecology of mast seeding in trees. *Biol J Linn Soc* 14:235–250
- Silvertown JW, Dodd M (1999) The demographic cost of reproduction and its consequences in balsam fir (*Abies balsamea*). *Am Nat* 136:154–166
- Sork VL, Bramble J, Sexton O (1993) Ecology of mast-fruiting in three species of North American deciduous oaks. *Ecology* 74:528–541
- Sperens U (1996) Is fruit and seed production in *Sorbus aucuparia* L. (Rosaceae) pollen limited? *Ecoscience* 3:325–329
- Sperens U (1997) Long-term variation in, and effects of fertiliser addition on, flower, fruit and seed production in the tree *Sorbus aucuparia* (Rosaceae). *Ecography* 20:521–534
- Tappeiner JC (1969) Effect of cone production on branch, needle, and xylem ring growth of Sierra Nevada Douglas Fir. *For Sci* 15:171–174
- Willson MF (1986) On the costs of reproduction in plants: *Acer negundo*. *Am Midl Nat* 115:204–207
- Yamaguchi DK (1991) A simple method for cross-dating increment cores from living trees. *Can J For Res* 21:414–416
- Yasumura Y, Hikosaka K, Hirose T (2006) Resource allocation to vegetative and reproductive growth in relation to mast seeding in *Fagus crenata*. *For Ecol Manage* 229:228–233
- Żywiec M, Holeksa J (2012) Sprouting extends the lifespan of tree species in a seedling bank: 12-year study. *For Ecol Manage* 284:205–212
- Żywiec M, Ledwoń M (2008) Spatial and temporal patterns of rowan (*Sorbus aucuparia* L.) regeneration in West Carpathian subalpine spruce forest. *Plant Ecol* 194:283–291
- Żywiec M, Holeksa J, Ledwoń M (2012) Population and individual level of masting in a fleshy-fruited tree. *Plant Ecol* 213:993–1002
- Żywiec M, Holeksa J, Ledwoń M, Seget P (2013) Reproductive success of individuals with different fruit production patterns. What does it mean for the predator satiation hypothesis? *Oecologia* 172:461–467