



Declining fruit production before death in a widely distributed tree species, *Sorbus aucuparia* L.

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Abstract

• **Key message** Trees are commonly thought to increase their seed production before death. We tested this terminal investment hypothesis using long-term data on rowan trees (*Sorbus aucuparia*) and found no support. Rather, seed production declined significantly before death, which points to the potential detrimental effects of reproductive senescence on regeneration in stands of old trees.

• **Context** Aging poses a fundamental challenge for long-lived organisms. As mortality changes with age due to actuarial senescence, reproductive senescence may also lead to declines in fertility. However, life history theory predicts that reproductive investment should increase before mortality to maximize lifetime reproductive success, a phenomenon termed terminal investment.

• **Aims** To date, it is unclear whether long-lived, indeterminately growing trees experience reproductive senescence or display terminal investment.

• **Methods** We investigated fruit production of rowan (*Sorbus aucuparia* L.), widely distributed trees that live up to 150 years, as they approached death.

• **Results** In our study population in Poland's Carpathian Mountains, 79 trees that died produced up to 20% fewer fruits in the years before their demise compared to 199 surviving trees of the same population.

• **Conclusion** The pattern of reproductive investment in *S. aucuparia* is suggestive of age-independent reproductive senescence rather than terminal investment. These findings highlight that the understanding of the generality of life history strategies across diverse taxa of perennial plants is still in its infancy.

Keywords Reproductive trade-offs · Fruit production · Senescence · *Sorbus aucuparia* · Terminal investment · Rosaceae

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Contribution of the co-authors MBP, MB, and MZ conceived the idea; ML and MZ collected the data; MBP and WDK analyzed the data; MBP wrote the first draft and all authors edited and approved the final version of the manuscript.

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1 Introduction

Life history theory posits fundamental trade-offs among survival, growth, and reproduction (Fisher 1930; Stearns 1976). In long-lived, iteroparous organisms, reproductive effort is therefore hypothesized to increase as the probability of survival declines during senescence, a phenomenon termed terminal investment (Clutton-Brock 1984; Williams 1966). In contrast, reproductive senescence, the decline in fertility with age, may occur as a corollary of whole-organism senescence (Thomas 2013). The terminal investment hypothesis has been supported by data on diverse animal taxa, spanning from beetles to humans (Creighton et al. 2009; Tifferet and Kruger 2010), but several exceptions exist (Jones et al. 2014; Yoccoz et al. 2002). In iteroparous perennial plants, senescence on the tissue- and organ-level is common, but whole-plant senescence may play only a minor role in determining the fertility of trees (Baudisch et al. 2013; Munné-Bosch 2008; Pedersen 1998). Therefore, reproductive senescence in plants could occur in parallel or independent of actuarial senescence—the age-related increase of mortality. Similarly, terminal investment may occur late in life despite an overall pattern of reproductive senescence. Despite broad interest in aging and senescence, however, the universality of the phenomenon across the tree of life as well as the underlying physiological and evolutionary mechanisms driving these phenomena are currently subject to debate (Baudisch et al. 2013; Jones et al. 2014; Munné-Bosch 2008).

Studies of reproduction in individually marked plants suitable for addressing these issues are scarce and only three studies have directly tested for reproductive senescence or terminal investment in sexually reproducing plants. In the first, Shefferson and Roach (2013) found that *Plantago lanceolata* L., a short-lived perennial, declined in both growth and reproduction over time, not directly as a function of age, but rather when considered relative to the time of their demise. In a second study, Koenig et al. (2017) found no evidence for changed investment in absolute or relative growth or reproduction in five species of North American oaks (*Quercus* spp.) before their natural death. There is, however, evidence for reproductive senescence in the tree *Populus tremuloides* Michx., in which clone age is associated negatively with relative pollen production and viability (Ally et al. 2010).

In lieu of individual-based data, population-based projection matrices of fertility and mortality as a function of age have been investigated for patterns of senescence. The demographic trajectories derived from the matrices suggest that fertility in two tree species, *Quercus rugosa* Née and *Avicennia marina* Forssk., increases with age,

while mortality decreases (Jones et al. 2014; Salguero-Gómez et al. 2015). The underlying projection matrices, however, are based on less than 10 years of data and do not account for individual reproductive behavior before death. In summary, our understanding of life history trade-offs and whole-plant senescence in plants is still rudimentary, despite considerable attention (Jones et al. 2014; Munné-Bosch 2015; Salguero-Gómez et al. 2013, 2016; Sletvold and Ågren 2015; Thomas 2013) and the popular belief that terminal investment is widespread in trees (Wohlleben 2016).

In this study, we analyze reproductive investment before death in rowan (*Sorbus aucuparia* L.), one of the most common trees bearing fleshy fruits in Europe, using long-term fruit production data (16 years) for 278 trees. Classic life history theory predicts increased reproductive effort with increasing mortality rate during senescence, because trees should allocate resources to reproduction rather than growth (Clutton-Brock 1984; Williams 1966). Because of the indeterminate growth of the trees, however, fruit production could simply vary as a function of tree size associated with age (Koenig et al. 2017). Similarly, individuals often vary in their fruit production due to site-specific abiotic conditions, such as microhabitat temperature or access to water (Barringer et al. 2013; Pesendorfer et al. 2016). Increased fruit production before death would therefore support the terminal investment hypothesis, while a decline would provide evidence for reproductive senescence.

We conducted reverse-age analyses to determine whether fruit production changed significantly in the years before death (Shefferson and Roach 2013). In addition to comparing raw fruit counts to trees paired for size and overall fruit production, we also analyzed relative crop size, a measure that scales an individual tree's counts to its maximum fruit production. The latter allows for the comparison of the proportional reproductive effort each plant displayed in a year, and controls for individual differences in overall productivity (Pesendorfer et al. 2016).

2 Materials and methods

2.1 Study species

S. aucuparia is a small to medium-sized (15–20 m), deciduous, fleshy-fruited tree species in the family Rosaceae with a broad distribution throughout northern Eurasia (Raspé et al. 2000). It has a maximum life span of ~150 years and fruit production starts at ~15 years (Grime et al. 1988). Population-level fruit production is highly synchronous and shows moderate to high

interannual variation (Satake et al. 2004; Sperens 1997; Żywiec et al. 2012). A 12-year study in our population revealed no trade-off between fruit production and radial growth increment, suggesting that resource limitation per se does not inhibit reproductive effort in *S. aucuparia* (Żywiec and Zielonka 2013). However, life history trade-offs in long-lived plants are often complex and non-linear (Knops et al. 2007; Sletvold and Ågren 2015) and lagged trade-offs may also occur in these mast-fruiting plants (Żywiec and Zielonka 2013).

2.2 Study site and data collection

The study was conducted in a 27-ha plot (564 × 480 m, 1170–1310 m a.s.l) in the Babia Góra massif of Western Carpathian Mountains (Żywiec et al. 2012). In this subalpine spruce forest, *S. aucuparia* occupies tree stand gaps caused by windstorms and bark beetle outbreaks (Holeksa et al. 2017; Żywiec and Ledwoń 2008). In 2000, all 365 trees with diameter at breast height (DBH) > 4 cm were mapped and marked, and subsequent fruit production was recorded during annual visits in September before fruit removal by birds was initiated. To estimate annual fruit production, we counted all the infructescences on a tree using binoculars. This number was then multiplied by the mean number of fruits counted on five infructescences of that individual in that year to obtain the total estimate (Żywiec et al. 2012; Pesendorfer et al. 2018). For our analysis, we selected a subset of trees ($n = 278$) according to the following criteria: (1) trees had to have produced fruits at least once during the study period (2000–2015); (2) trees were large enough to consistently produce fruits (DBH > 7 cm); and (3) trees for which we had a minimum of 5 years of data.

2.3 Statistical analysis

We used reverse age analyses to test the terminal investment hypothesis that fruit production increases as an organism approaches death (Hammers et al. 2012; Martin and Festa-Bianchet 2011). Reverse age analyses provide a comparison of longitudinal data for individuals that have died to surviving individuals to determine the difference in fruit production patterns as a function of remaining time to death (Shefferson and Roach 2013). We considered the year of death that in which we first noted the tree's death during fruit surveys in September based on the absence of live leaves. For each of the years preceding death, we matched the tree's fruit production with that of paired healthy individuals. Paired individuals were selected from trees with matching DBH to account for size (there were often multiple trees of the same size) and by choosing the

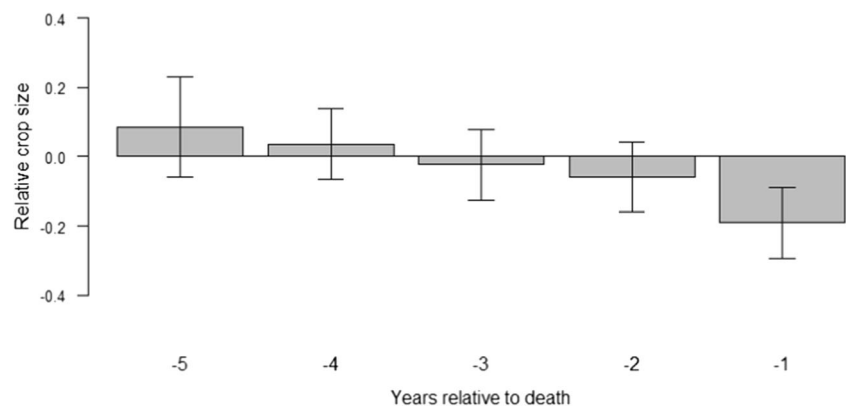
tree with the closest maximum value in fruit production (in the whole data set) to account for other factors that could affect fertility. To conduct reverse age analyses, we constructed a generalized linear mixed model using the package *glmmTMB* version 0.1.3 in R version 3.4.4 (Brooks et al. 2017; Magnusson et al. 2017; R Core Team 2018). Due to the large number of zeros in the fruit counts, we constructed zero-inflated generalized linear mixed models (GLMMs) with negative binomial error distributions (“nbinom2”) for the absolute fruit production estimates. The model contained the number of years before death and its interaction with the outcome (dead/alive) as fixed effects, where the interaction term allows us to test the hypothesis that seed production in trees that eventually died was different from that of trees that continued living after the 5-year comparison period. Finally, tree identity and calendar year of death were included as random effects to account for individual history and population-wide variation due to mast-fruiting (Koenig et al. 2017; Shefferson and Roach 2013).

To account for possible effects of the large inter-annual variation in population-level fruit production (i.e., mast-seeding), we conducted a second, separate analysis that investigated the difference in relative crop size between the mean of all surviving trees and ones that eventually died. To do so, we calculated relative fruit production values for each individual/year combination by scaling the annual count to the maximum count recorded for that individual, resulting in annual proportions of potential fruit production (Pesendorfer et al. 2016). We then calculated the mean relative crop size (RCS) of surviving individuals for each year and determined the degree to which trees that eventually died differed from these values (Δ RCS). To test whether the trees produced smaller RCS values as they approached death, we constructed a linear mixed model of Δ RCS of the 79 trees, with the years before death and tree size (DBH) as fixed effects. To control for repeated sampling, the model contained tree identity as a random effect. To illustrate the results, we present the effect sizes and 95% confidence intervals in Fig. 1. Full modeling results are presented in [Appendix](#).

Model fit was assessed by contrasting simulated model predictions with observed values using the *DHARMA* package version 0.1.6 and conducting Kolmogorov–Smirnov tests on the deviation of residuals from uniformity (Hartig 2018).

Finally, for basic comparisons of dead and surviving trees, we used Welch two sample *t* tests in the R base package (R Core Team 2018). In addition to DBH, maximum, mean, and relative seed crops, we also compared the autocorrelation and variability of seed production. For the last two comparisons, we used data on the

Fig. 1 The difference in relative crop size between dying ($n = 79$) *S. aucuparia* trees and the mean for the healthy population ($n = 199$) 5 years preceding death. Effect sizes ($\pm 95\%$ confidence intervals) from linear mixed models of differences in crop size between trees that eventually died and paired surviving trees of matching size and similar maximum seed production. See Table 2 for full model results



last 5 years before death and compared it to the last 5 years of the study in surviving trees.

3 Results

Of the 278 *S. aucuparia* trees that met our selection criteria, 79 (28.4%) died between 2004 and 2015 after five or more years in the study (6.5 ± 0.8 deaths per year; range 3–13). The size of the deceased trees was significantly smaller than that of surviving trees, but the mean difference in DBH was only 1.5 cm (dead 12.4 ± 3.2 cm; alive 13.9 ± 4.0 cm; t test $t = -3.3$, $df = 177.4$, $P = 0.001$). Similarly, trees that died had lower maximum fruit production values (fruit crops dead 3308 ± 623 alive $14,103 \pm 1078$; $t = -8.7$, $df = 274.6$, $P < 0.001$), but higher mean relative crop sizes (dead $21.4 \pm 8.7\%$; alive $16.8 \pm 5.6\%$, $t = 4.4$, $df = 104.9$, $P < 0.001$).

For trees that died, fruit production declined in their final years, both in absolute and relative terms. The reverse age analysis of full fruit crops shows that 63 (79.7%) trees failed to produce any fruits in the year before their death. The GLMM results indicate that this number is significantly higher than expected from the distribution of the data (Table 1 in Appendix). Furthermore, the reverse age analysis of relative crop sizes indicated that trees approaching their demise showed reduced fruit crops in comparison to all the surviving trees in the study population (Table 2 in Appendix). Relative fruit production in the final year preceding death was reduced by $19.1 \pm 5.2\%$ compared to the healthy trees in the population (Fig. 1). The mean variability of seed production over the last 5 years before death did not differ from that of live trees over the last 5 years of the study ($CV_{\text{dead}} = 167.4 \pm 43.1$ (mean \pm SD), $CV_{\text{live}} = 165.9 \pm 35.2$, t test $t = 0.27$, $df = 107.36$, $P = 0.78$), but we found a lower negative autocorrelation with the previous years' seed production ($ACF1_{\text{dead}} = -0.24 \pm 0.26$, $ACF1_{\text{live}} = -0.35 \pm 0.13$, t test $t = 3.4$, $df = 84.7$, $P < 0.001$).

4 Discussion

We found evidence that suggests a decline in reproductive investment in *S. aucuparia* trees before death. Trees nearing death produced nearly 20% less of their potential fruit crop than similar surviving trees. This effect was only found for the year before death, however.

There was no evidence for terminal investment in the fruit production. Overall, evidence from the three studies that have been conducted thus far, including this one, suggests that terminal investment, although common in animals, may not occur in plants. The paucity of available data on this phenomenon highlights how difficult it is to test this hypothesis and the need for further research. In fact, despite an increase in whole-plant senescence research, little attention has been paid to the effects of aging on fruit production, despite its central role in energy allocation trade-offs (Munné-Bosch 2015; Salguero-Gómez et al. 2013; Thomas 2013).

The only other study on the reproductive behavior of individual trees before death found no difference in reproductive investment as the oaks that were studied approached their demise (Koenig et al. 2017). One potential explanation for this negative result is that tree death may be a prolonged process, particularly in oaks that can live for centuries (Pedersen 1998). In our case, the maximum lifespan of *S. aucuparia* trees is substantially shorter, on the order of 150 years, which is reflected in the high proportion of trees (28.4%) that died during the 16 years of the study. This shorter lifespan likely allowed us to capture a larger proportion of the trees' lifetime and decline in reproduction. In trees with longer lifespans, Munné-Bosch (2015) suggests that the mere likelihood of an accidental exogenous death that comes with long life may mask senescence before it is an observable phenomenon. Faster growing trees, such as *S. aucuparia*, may thus hold the key to understanding actuarial senescence in trees. The fact that we only detected reduced reproductive effort in the final year suggests that reproduction may only cease shortly before trees are no longer able to physically maintain the soma. Our finding of less negative autocorrelation in seed

production further suggests that cyclic dynamics based on resources collapse before death.

The understanding of life history strategies in plants has made considerable advances in recent years (Adler et al. 2014; Salguero-Gómez et al. 2016), but theory still relies on few well-studied examples. For example, Jones et al. (2014) compared the basic relationship between aging, fertility, and mortality across taxa spanning the range of multicellular organisms and found a diversity of mortality patterns across age, even within species. This finding poses a challenge to the notion that whole-organism senescence may be an evolved trait, as suggested by Medawar (1952) and Williams (1957), that relies on mechanisms similar to the tissue- and organ-level senescence observed in leaves and other plant structures (Hamilton 1966; Munné-Bosch 2008). In animals with determinate growth, the separation of soma and germline may result in differential allocation of energy to reproduction (terminal investment) as soma maintenance becomes pointless or too costly, as suggested by the disposal soma theory (Kirkwood 1987; Weismann 1893). For modular, long-lived, indeterminately growing species, terminal investment may not represent the optimal reproductive strategy. While some models for energy allocation in iterparous perennial plants predict increased allocation of energy to reproduction with increasing age (Kozłowski 1993), others predict that deciduous trees, such as that studied here, will only invest excess energy into reproduction rather than exhibit a trade-off (Iwasa and Cohen 1989).

The latter scenario may well apply in *S. aucuparia*, whose fruit production strategy appears to be opportunistic in the sense that the production of large fruit crops is restricted to years of favorable conditions, when more energy is obtained than necessary for normal growth and maintenance. Since the trees flower after leaf development and initiation of photosynthesis, flower production and subsequent fruiting may vary mostly with current and previous year conditions (Fernández-Martínez et al. 2015; Pearse et al. 2016; Żywiec et al. 2012). Under such conditions, an optimal, long-term strategy of reproductive allocation may not involve terminal investment.

If the signature of changes in reproductive strategies near death is more subtle, refined approaches in the field and during data analysis may be required in order to provide more convincing evidence for this phenomenon. The measure of seed production used in this study provides a somewhat coarse estimate of reproduction and ignores the viability or pre-dispersal predation of fruits (Żywiec et al. 2018). Similarly, despite significant advances in statistical modeling of zero-inflated count data and the development of novel approaches to modeling mast-seeding in plant populations (Vacchiano et al. 2018), real-world data sets provide analytical challenges

when addressing hypotheses that predict effects over multiple years.

It is possible that definitive answers regarding the types of trade-offs occurring in long-lived, iteroparous plants will not be found until a more substantial body of studies exists to examine the generality of life history strategies across larger sample of species. Nonetheless, our study sheds further light on the phenomenon of terminal investment and suggests that long-lived trees do not escape senescence as fruit production declines at the end of their lives.

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Data availability The data is publicly available at FigShare (Pesendorfer et al. 2018). Data set not peer-reviewed. Pesendorfer MB, Bogdziewicz M, Koenig WD, Ledwoń M, Żywiec M (2018) Data for “Declining fruit production before death in a widely distributed tree, *Sorbus aucuparia* L.”. V1. FigShare. [Dataset]. <https://doi.org/10.6084/m9.figshare.7330052.v1>

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix. Expanded modeling results

Generalized linear mixed model of seed count estimates contrasted with paired trees

The models were constructed using the package *glmmTMB* 0.1.3 in *R* version 3.4.4 (Brooks et al. 2017; Magnusson et al. 2017; R Core Team 2018). Because the seed count data was zero-inflated and overdispersed for Poisson error distributions, we constructed a zero-inflated negative binomial GLMM with the fixed effects “year before death” (categorical), “dead (yes/no)” (categorical), their interaction, as well as “DBH” (continuous) and random effects of “individual” to control for repeated sampling and “year of death” to account for mast-seeding. Excluding DBH resulted in $\Delta\text{AIC} = 60.1$ despite the reduced degrees of freedom. Because we hypothesized that the drivers of the additional zeros were the same as the ones of low counts, we used the same model structure for both the zero-inflation and the conditional model (Zuur et al. 2009). We assessed model fit by comparing the outcome of 1000 simulated model responses to the observed responses using the package DHARMA (Hartig 2018). The Kolmogorov–Smirnov test revealed that simulated residuals did not deviate from uniformity ($D = 0.22$, $P = 0.85$).

Table 1 Results of the reverse age GLMM of paired seed counts: (A) zero-inflation model and (B) conditional model. Parameter estimates, standard errors, z values, and P values. ($n = 770$)

Parameter	Estimate	SE	z	P
A) Zero-inflation model				
Dead	-0.171	0.350	-0.489	0.625
DBH	-0.122	0.027	-4.515	<0.001
Year-4	-0.122	0.349	-0.350	0.726
Year-3	0.182	0.343	0.531	0.595
Year-2	0.347	0.342	1.015	0.310
Year-1	-0.292	0.353	-0.828	0.408
Year-4 × dead	0.004	0.450	0.008	0.994
Year-3 × dead	-0.000	0.489	-0.001	0.999
Year-2 × dead	0.737	0.487	1.511	0.131
Year-1 × dead	2.483	0.529	4.695	<0.001
B) Conditional model				
Dead	0.253	0.284	0.893	0.372
DBH	0.218	0.030	7.442	<0.001
Year-4	-0.060	0.295	-0.201	0.841
Year-3	0.351	0.299	1.174	0.241
Year-2	0.204	0.319	0.638	0.523
Year-1	0.036	0.283	0.129	0.898
Year-4 × dead	0.197	0.398	0.496	0.620
Year-3 × dead	-0.239	0.400	-0.597	0.551
Year-2 × dead	-0.026	0.437	-0.061	0.952
Year-1 × dead	-0.066	0.505	-0.131	0.896

Linear mixed model of relative seed crop contrasted with the healthy population

To investigate the differences in relative seed production between dead and surviving trees independent of annual variation in population-level seed production, we calculated the annual mean relative seed crop for all surviving trees and for each tree that eventually died, we calculated the difference in relative seed production Δ RCS to the population mean. This provides a data set of 5 years of Δ RCS values for 79 trees. We constructed a linear mixed model of Δ RCS values with the fixed effect “year before death” (categorical) and the random effect “individual” to control for repeated sampling. Excluding the fixed effect “DBH” did not improve model fit in terms of AIC (Δ AIC = 1.9). However, including the parameter improved the ability of the model to predict observed values, as illustrated by the non-significant Kolmogorov–Smirnov test (see below). The model was not overdispersed (dispersion estimate for Gaussian family $\sigma^2 = 0.102$). An Kolmogorov–Smirnov test of the model residuals shows that the assumption of uniformity was not violated ($D = 0.067$, $P = 0.066$).

Table 2 Results of the reverse age LMM of relative crop sizes of trees that died. ($n = 385$ observations)

Parameter	Estimate	SE	z	P
DBH	0.001	0.005	0.270	0.787
Year -4	0.036	0.052	0.699	0.485
Year -3	-0.024	0.052	-0.457	0.648
Year -2	-0.060	0.052	-1.156	0.248
Year-1	-0.191	0.052	-3.708	<0.001

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