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Demographic senescence and effects on population dynamics of a perennial plant

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Abstract. Demographic rates in plants are usually assumed to be more stage or size dependent than age dependent, and aging is therefore not considered in demographic models. However, little is known about how aging of individuals may affect population dynamics. We present analyses of demographic data for three populations of Fumana procumbens collected 1985–2013, on individuals with known year of germination. We modeled age- and size-dependence of the vital rates of survival, growth, fruiting probability, and fruit number using thin plate spline regressions, and constructed an age × size integral projection model (IPM) to project population-level effects of aging. We found strong correlations between age and vital rates in solely age-based vital rate models, where vital rates initially increased with age, after which they stabilized and, in some cases, eventually declined. In survival models with both age and size, the effects of age were statistically significant, whereas size effects were insignificant at two of the sites. For other vital rates, most of the effect of age could be explained by size alone. In addition, including the age effects on survival in the IPM led to lower population growth rates compared to predictions of a size-only IPM. These results illustrate that demographic senescence does occur in perennial plants, which has only been demonstrated clearly in a few recent detailed studies. Moreover, we show that population projections may be overly optimistic if they do not consider plant age. We conclude that the possibility of demographic senescence should be considered in demographic population models, such as those used in viability analyses of threatened species.

Key words: actuarial senescence; age × size; aging; Fumana procumbens; integral projection model; plant demography; vital rates; whole-plant senescence.

INTRODUCTION

Demographic rates in perennial plants are usually thought to be more size dependent than age dependent, and most plant demographic studies do not consider plant age (Menges 2000, Caswell 2001). However, relatively little is known about aging in plants, including whether plants generally undergo demographic senescence, a deterioration in fecundity and/or survival with advancing age (but see Gibson et al. 2013, Munné-Bosch 2015, Dahlgren and Roach 2017). If plants show demographic, or “whole-plant” senescence, then it is likely that this influence of age on demographic (vital) rates needs to be accounted for in studies of plant life history and drivers of plant population dynamics. That is, if vital rates are modeled as only size dependent, when in fact they are affected by age as well, demographic parameters such as life expectancy or extinction risk may be over- or underestimated. In this paper, we evaluate effects of age on vital rates, and how accounting for age impacts the asymptotic population growth rate and related parameters (stochastic and transient growth rates), which are central for ecological and evolutionary demography.

One of the main reasons for the lack of knowledge about demographic consequences of aging in perennial plants is that there have been few studies collecting data on individual plants over time periods that are long in relation to the average life span of the study species (Dahlgren and Roach 2017). There are across-species comparative studies that have calculated age-specific parameters from size data (e.g., Silvertown et al. 2001, Horvitz and Tuljapurkar 2008), and some evidence of senescence in trees because of negative effects of size (Mencuccini et al. 2005, Baudisch et al. 2013, Dahlgren and Roach 2017). However, the long-term studies that do exist show conflicting results regarding how age affects fecundity and survival. Several studies indicate
no or negligible senescence in plants (Harper and White 1974, Rose et al. 1998, Hutchings 2010, Dahlgren et al. 2016c), but there are also recent studies that have found evidence of demographic senescence (Pico and Retana 2008, Roach et al. 2009, Dahlgren et al. 2016b, Quarles and Roach 2018). It has been suggested that some plants may even show “negative senescence,” an increasing survival probability after the onset of reproduction (Vaupel et al. 2004). Clearly, there is a need for more long-term studies to determine how plants in general age.

Demographic population models, such as matrix models (Caswell 2001) and integral projection models (IPMs; Ellner and Rees 2006), are widely used to predict population-level processes based on average vital rate trajectories over state variables such as size and age. However, these models are also most often structured only by size, not by age (but see, e.g., Garcia et al. 2011, Chu and Adler 2014), and general effects on population dynamics of including age are thus unknown. A key parameter for demographic analyses is the deterministic, or asymptotic, population growth rate ($\lambda$), that is, the dominant eigenvalue of the matrix (kernel) of the models. The deterministic population growth rate has been found to be affected by including survival increases in young plants (Chu and Adler 2014), but we still need more empirical information about how demographic senescence in vital rates may affect $\lambda$. If $\lambda$ is lowered by incorporating age effects, then it would be interesting to also assess effects on the stochastic population growth rate (Tuljapurkar 1989) and transient growth rates (e.g., McDonald et al. 2016), to evaluate whether age effects are impacted by environmental variation and the current age structure, respectively.

Here we present novel analyses of long-term demographic data collected on plant individuals observed germinating between 1985 and 2013 at three study sites on the Baltic island Öland in Sweden, for the nonclonal perennial dwarf shrub *Fumana procumbens*. We determine whether there are negative effects of age on individual survival, growth and/or fecundity, while taking individual size into account. We also construct age × size IPMs calculating deterministic, transient, and stochastic population growth rates to analyze population-level effects of aging. We address the following hypotheses:

1) Survival, plant size and reproduction of established plants initially increase with age until a certain age is reached, after which they stabilize and eventually decline.
2) Projections of growth rates using demographic population projection models will be overly optimistic if age effects are not included in addition to effects of size.

**Materials and Methods**

**Study plant**

*Fumana procumbens* (Cistaceae) is a perennial dwarf shrub growing in open, often south-facing slopes with calcareous soils at the study sites. It is not clonal, and all shoots originate from one main stem, which simplifies identifying individuals in the field. In addition, it has a short dispersal range, which means that that most plants originate from the same population, or patch (Bengtsson 1993). The species has its main distribution in southern Europe, but populations exist on the alvar grasslands on the islands Öland and Gotland in Sweden (Hultén 1971). It occurs on well-drained, dry soil, with roots growing in crevices in the bed rock to reach water (Hegi 1925, Pettersson 1958).

Only sexual reproduction has been reported, with self-fertilization as the dominant strategy (Vestergren 1909, Pettersson 1958). The fruit is a capsule with 5–10 seeds. Capsules and seeds typically fall directly beneath the mother plant, but may also be dispersed by wind or ants (Bengtsson 1993). Average life-span based on size-based matrix approximations has been estimated as 18.9 yr for individuals that survive to flowering (Ehrén and Lehtilä 2002). Population sizes in the study area fluctuate in response to yearly variation in weather, but are also regulated by negative intraspecific density dependence (Dahlgren et al. 2016a).

**Study sites**

The study sites are located within an 0.7 × 0.5–km area in the northeastern part of the alvar grassland Stora Alvaret on Öland in Sweden. The distribution of *Fumana* at the sites is patchy on low ridges and in sheltered microsites around an area of karst limestone. Three sites were chosen to represent different habitat types and grazing regimes (Bengtsson 1993). Site Prästgropen (PG) is open, wind-exposed, and partially shaded by higher vegetation. Soil depth varies because of combinations of deep fissures, open limestone, and weathering soils. There is a relatively dense vegetation cover in the field layer, dominated by vascular plants with a high proportion of grasses and sedges. Grazing and trampling by cattle occur in the area. Site Ekelunda (EK) represents a more variable vegetation. Surrounding shrub vegetation provides some shading and partial shelter from the wind. The site’s field layer consists largely of vascular plants with lichens being more abundant than site PG. Very little cattle grazing occurs. Site Tornröra (TO) has extensive fissured limestone covered with thin soil and provides the highest number of suitable crevices where individuals can develop a long taproot and have the opportunity to become large and highly reproductive. The site is well sheltered from wind but more exposed to the sun and has a higher proportion of mosses and lichens. Grazing and trampling occur more seldom and irregularly. Age distributions, size distributions, and reproductive output of *Fumana* vital rates vary among these sites (Appendix S1: Table S1).
Data collection

Within the study area, 33 permanent 0.5 × 0.5–m plots were established at spots where plants were growing. Data were collected in August each year 1985–1995, 1997–1999, and 2007–2013. Between 1985 and 1995, all plots were examined. From 1998, disturbances due to a restoration project between 1998 and 2002 led to some plots being lost or not being possible to locate some years. The number of available plots has since varied between 14 and 27.

Demographic data were collected for all individuals in each plot, with newly established individuals included as they sprouted. Number of fruits (capsules) was counted for each reproductive plant and total branch length (hereafter size) for each plant estimated from depictions on 1 : 4 scale maps. Presence or absence of each previously recorded individual was noted. Plant size was only recorded between 1989 and 2012. This data were previously used to study environment- and density-driven population dynamics using size-based IPMs (Dahlgren et al. 2016a). In the present study, we only used data for individuals with known year of germination and known size to investigate effects of age on vital rates and population dynamics, that is, data between 1989 and 2012. Data from 1985–1988 were only used to calculate age from germination year, and data from 2013 were only used to determine death year. With these criteria, data for 595 individuals were available.

Plant germination and death during years when data were not collected were assumed to occur at the midpoint of the missing data time period. For these periods, germination and mortality of young plants are thus underrepresented, but our analyses are independent of exact germination rates, and there is still sufficient data on survival and growth of young plants from the other years.

Analysis and modelling

We modelled the vital rates survival, growth of surviving plants, fruiting probability, and fruit number for reproducing plants using thin plate spline regressions in the package ‘gamm4’ (Wood and Scheipl 2017) for R version 3.4.2. This type of model relaxes the assumption of linearity in regression models and allowed us to investigate possibly nonmonotonic age trajectories of vital rates without specific functional forms. Model complexity is automatically penalized to avoid overfitting, and random effects can be included. Survival and fruiting probability were modeled using logistic regressions, growth was modeled using Gaussian regression, and fruit number was modeled using negative binomial regression (log link function). The dimension of the basis used to represent the smooth term in gamm4 was set to \( k = 5 \), to limit maximum curve complexity. For survival and fruiting probability, we used \( k = 4 \) in models with age, size, and density, as the models otherwise did not converge. Random intercepts among years, plots and individual plants were included in all models. This was done to account for repeated measurements and data structure, and to account for yearly fluctuations of environmental factors, which have previously been found to affect vital rates (Dahlgren et al. 2016a). Different vital rate trajectories were allowed among sites, using the ‘by’ argument in the ‘s()’ function in gamm4.

We fitted vital rate models with only age (years) and with both age and size (summed branch length) and compared the effect of age on vital rates. Because density might influence the age structure, we also fitted models including intraspecific density, estimated as total branch length per plot divided by the maximum observed branch length per site, that is, as a proportion of assumed maximum carrying capacity, to test whether age effects changed. As this inclusion of density did not influence the effects of age notably, density effects were disregarded from further analysis and are not presented. In addition, we fitted models including interactive effects between age and size, as tensor products using the t2() function in gamm4. These models often did not converge because of their complexity and are therefore not presented, but in models that did converge, the presence of the interactions did not change the total effect of age notably. We considered relationships statistically significant at \( P < 0.05 \). \( P \) values were based on Wald tests using the summary.gam function in the mgcv package (Wood 2013).

We used the fitted vital rate models for all three sites as components of an age × size IPM (Ellner and Rees 2006). Age was divided into 19 categories corresponding to the ages 1 to 19+ (the oldest plant found), with the last category consisting of all ages equal to and above 19. This extrapolates age effects for the EK site, as the oldest plant in this site reached an age of 11 yr. However, results for EK were similar when we included only 11 age classes. IPMs can be viewed as an extension of matrix models, where individuals do not necessarily move between discrete classes over time steps (years), but their state can also be described with continuous variables (typically size, as here). IPMs are straightforward to parameterize with regression models even when including additional state variables (as age in this case). Our model described the annual life-cycle transitions of *Fumana procumbens* with continuous kernels giving size transitions for each age class, with code adapted from Ellner and Rees (2006) and Garcia et al. (2011). All individuals that survive increase 1 yr in age, and we thus described the age and size demography of *Fumana* with 19 IPM kernels for ages 1–19. In addition to the four vital rates modeled using the regression models, we estimated average germination rate and size distributions of seedlings from the data. Germination rate was calculated for each site from total number of seedlings divided by total number of capsules during the entire experimental period. To test the importance of each vital rate for model.
predictions, we added age to one regression model in the IPM at a time and compared the results.

To investigate to what extent age effects on vital rates affected population projections, we calculated deterministic, stochastic, and transient population growth rates, considering potential differences among these three commonly calculated measures. We expected that effects of demographic senescence would be more pronounced in stochastic growth rates than in deterministic growth rates, because random fluctuations of vital rates across years generally lower growth rate and may make it more sensitive to negative effects of age. Transient growth rates depend on the current population structure, and this growth rate may, for example, be more (less) sensitive to negative age effects on vital rates of old individuals, if there are more (less) old plants than in the stable age distribution. Calculations were made for models parameterized with regressions including age and size effects, and for models parameterized with regressions including only size effects. The deterministic population growth rate ($\lambda$), the long-term growth rate eventually reached in a model using a constant kernel, was calculated by iteration until the fifth decimal of $\lambda$ was the same as in the previous iteration. Stochastic population growth rate was calculated by randomly drawing a kernel representing a certain yearly transition, calculated from the random year effects in the vital rate models, repeating this process 10,000 times, and taking the geometric mean of the 10,000 growth rates. We also calculated the variance of the stochastic growth rate. Transient population growth rate was calculated by iterating the models with constant mean kernels for 20 yr, starting with the observed age and size distributions in the final year of the data and taking the geometric mean of the resulting yearly growth rates.

For vital rates where possible senescence effects were found in the gamm models, that is, for survival, we

![Survival of Fumana procumbens individuals as a function of age at the three sites (Prästgropen (PG), Tornröra (TO), and Ekelunda (EK)) and for all sites pooled, without (W/O) or with (W) size the previous year as a covariate. Age trajectories for models including size are for individuals of average size. The decrease following the highest survival value is statistically significant for all sites (see Appendix S1: Table S3). Shaded polygons indicate standard errors. $n$ equals number of plant individuals.](image-url)
performed additional statistical analyses to corroborate that the data supported declines with age for high ages. First, we fitted linearized models of survival for only age spans where gamm curves were decreasing. We also fitted mixed effects logistic regression models with first, second and third polynomial degree age and size terms, utilizing all data, and tested the significance of the polynomial terms. In addition, we compared IPM kernels corresponding to different survival models to distinguish between effects of demographic senescence per se and other effects of including age. We first compared integral projection models with and without age where survival was modeled with generalized linear models (i.e., where survival is modeled as a logistic curve, and thus cannot decrease following an increase). We also compared these IPMs with IPMs based on the nonlinear (gamm) survival models. However, the latter comparison may not be a good method of testing effects of senescence, because the curves can differ in shape for younger ages too. As an alternative method of determining the effect of senescence per se, we used IPMs where survival followed the gamm (and by extension also the polynomial) curves, until maximum survival was reached, and then used that survival value for each following age. This overestimates total survival but is a straightforward way to calculate the effect on $\lambda$ of the observed declines in survival for old ages.

RESULTS

Age had a significant and similar impact on survival both with and without size in the model (Fig. 1). There were considerable differences between sites, with survival probability of plants at sites TO and EK increasing with age until around an age of 5–7 yr, followed by a decline with age in older plants, as hypothesized. At site TO and when data from all sites were pooled, survival probability tended to stabilize or increase again for very old plants (over 12–13 yr). At site EK, survival was lower in general, and there were

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**Fig. 2.** Size of *Fumana procumbens* individuals as a function of age at three sites (Ekelunda [EK], Prästgropen [PG], and Tornrö [TO]) and for all sites pooled, without (W/O) or with (W) size previous year as a covariate. Age trajectories for models including size are for individuals of average size. Shaded polygons indicate standard errors. Note the varying ranges of $y$-axes.
no very old plants. Site PG showed a constant decrease in survival probability with age. Size was significantly correlated with survival at all sites in models with only size, but only remained significant at site EK, after accounting for age. The decrease in survival for old plants was supported also by statistically significant polynomial terms in glmm models, which yielded similar curves as the gamm models, and also similar population growth rates in the IPM (Appendix S1: Table S2, Figs. S1 and S2). In addition, slopes in models including plant data only from the declining period was significantly negative for all sites (Appendix S1: Table S3).

Age had a significant impact on size, fruiting probability, and fruit number in models with only age (Figs. 2–4), with vital rates generally increasing continuously with age, or stabilizing and in a few instances declining at high ages. However, most of the correlations between age and vital rates could be explained by size. The increase in fruiting probability with age at site PG, and for all sites pooled, were the only effects of age that were statistically significant in the presence of the size variable.

Including age as a second state variable in IPMs, in addition to size, led to lower deterministic, stochastic and transient growth rates for two of the three populations and when data for all populations were pooled (Fig. 5). At the third site (PG), growth rates were similar in models with and without age. Survival had the largest influence on the observed differences in population growth rates between models (Appendix S1: Fig. S3). Predicted stable age distributions were fairly close to observed distributions (Appendix S1: Fig. S4).

Model manipulations showed that effects of age-dependent survival on population growth rates were driven by the decline at old ages. In models where survival

![Fruiting probability of *Fumana procumbens* individuals as a function of age at three sites (Ekelunda [EK], Prästgropen [PG], and Tornör [TO]) and generally for all sites, without (W/O) or with (W) size as a covariate. Age trajectories for models including size are for individuals of average size. In models including size, only All sites and PG show significant increase with age ($P = 0.00186$ and $0.00202$, respectively). The decrease following the highest survival value is significant for all sites. Shaded polygons indicate standard errors. $n$ equals number of plant individuals.](image-url)
was kept constant after reaching its maximum value, predicted growth rates were generally as high as for models that did not incorporate age, at least when using pooled data (Appendix S1: Fig. S5). The stochastic population growth rate was 1.051 for the model without the decline, compared to 1.044 for the model without age and 1.019 for the model with the decline. In addition, although replacing the gamm survival models with generalized linear mixed models resulted in lower growth rates, differences in growth rates between models with and without age were generally negligible (Appendix S1: Fig. S6).

**DISCUSSION**

We found that survival of *Fumana procumbens* individuals generally increased with age for young plants, but that this was followed by a decrease in survival with age for older plants, indicating demographic, or actuarial, senescence. Moreover, predictions of population growth rate were generally lower in IPMs where age was accounted for in addition to size, and this effect was to a significant extent driven by the decrease in survival for old plants. Evidence for demographic senescence in plants has only rarely been reported previously, and we are not aware of any study showing that population projections by demographic models can be overly optimistic if negative effects of aging are not accounted for.

Our results are interesting in the context of understanding general patterns of aging in plants, in that they corroborate findings of a few recent detailed studies that report evidence of actuarial senescence (Pico and Retana 2008, Ruach et al. 2009, Dahlgren et al. 2016b), but also show substantial differences among populations. That plants show actuarial senescence is in line with predictions of classical evolutionary theories of aging, i.e., that no organism can escape senescence (Hamilton 1966). However, plants have long been thought to show negligible

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**FIG. 4.** Fruit number of *Fumana procumbens* individuals as a function of age at three sites (Ekelunda [EK], Prästgropen [PG], and Tornrör [TO]) and generally for all sites, without (W/O) or with (W) size as a covariate. Age trajectories for models including size are for individuals of average size. Shaded polygons indicate standard errors. A few individuals with fruit number >30 (EK and PG) or >50 (All sites and TO) are not presented. Note the varying ranges of y-axes. *n* equals number of plant individuals.
effects of aging (cf. Harper and White 1974), which has also been supported by recent studies (e.g., Rose et al. 1998, Hutchings 2010). Our results suggest that this variation in survival trajectories across studies may be caused by age effects also being driven by the environment (cf. Roach et al. 2009). For example, the site with a constant decrease in survival is more disturbed by both wind and cattle than the other sites, and high survival at low ages can be expected to be advantageous in such environments, even if it comes at a cost of lower survival of older plants (e.g., Dahlgren et al. 2016b). We also found evidence of effects of heterogeneity of individual frailty (Vaupel and Yashin 1985), in terms of increasing average survival at very old ages, but only at the site with the highest overall survival. Increases in the population average survival that are driven not by within-individual changes, but by the most fit individuals being more likely to survive to extreme ages, has previously been described for animals, including humans (Vaupel and Yashin 1985).

For vital rates other than survival, our results support the notion that plant demography is better viewed as size-structured than age-structured (Kirkpatrick 1984, Caswell 2001, Williams et al. 2006). However, the age effects we do identify indicate both that age can be a possibly better predictor than size for some vital rates (Lauenroth and Adler 2008, Pico and Retana 2008) and that age may contain additional information that is not captured by size. Age seemed to be a better predictor for survival than size, based on size effects not being statistically significant in most cases when age was accounted for. For fruiting probability, age was statistically significant when accounting for size at one site, showing a pattern of “negative reproductive senescence” (cf. Vaupel et al. 2004). However, when only age was included in the model, a surprisingly complex relationship was suggested. These changing relationships, caused by correlations between size and age, suggest that both variables should be considered as structuring variables for plant demographic rates.

The fact that incorporating negative age effects on survival affected IPM predictions of population growth rates has important implications for both theoretical and practical ecological applications of demographic modeling. Chu and Adler (2014) previously reported that models that ignore age could underestimate population growth rates, especially for populations with strong Type III survivorship curves. Our results, in which survival follows a Type III curve for young plants but then decreases for old plants, show that growth rates can also be overestimated unless age is accounted for. Moreover, we show that age effects were not notably affected by environmental variation or by the current age and size distributions. That is, despite stochastic and transient growth rates differing from deterministic growth rates, effects of including age were similar for all three rates. Taken together, these results have important implications for demographic analyses in general. For example, central demographic parameters such as reproductive values (Fisher 1930) and the elasticity of population growth rate to vital rates (de Kroon et al. 1986) both partly depend on the population growth rate. As a result, they can also be influenced by whether age is explicitly included in models. In conservation biology, a common approach of conducting population viability analysis for threatened species is to calculate extinction risks based on stochastic IPMs or matrix projection models (cf. Morris and Doak 2002). If including age leads to a lower stochastic growth rate, then it also means the extinction risk is greater than what would be predicted by a size-only model.

In conclusion, we recommend considering both age and size in plant vital rate models. In particular, our results entail that the possibility of demographic senescence should be considered when calculating population growth rates. More broadly, our results suggest that age effects, which have been neglected in plant demography, should again be considered by population biologists.

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Literature Cited
