

# 15 Demographic Senescence in Herbaceous Plants

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## Short Summary

For herbaceous plants, in contrast to many higher animals but similarly to other modular and sedentary life forms, it is not so much a question of how senescence progresses as it is a question of whether senescence occurs at all for most species. Overall, both the empirical evidence and theoretical predictions provide contrasting evidence. Monocarpic species and other semelparous life forms are an extreme example of senescence. For polycarpic, iteroparous plants, however, there is only limited evidence that senescence occurs at all. Our review of studies with herbaceous plants also shows that there are only a few studies with detailed age-based demographic data, and here too the evidence for senescence is limited. Moreover, the detrimental effects of ageing are hard to detect in the observational studies upon which most of our current knowledge is built. Our theoretical expectations suggest that it is likely that the evolutionary pressure that shapes senescence in other organisms also acts on plants, but there are also several aspects of plant biology that conflict with some of the assumptions in classical models of the evolution of senescence.

## Introduction

### Definitions

We use the term 'senescence' to mean detrimental changes in physiology and increased risk of death as organisms age. This has sometimes been called 'whole-plant senescence' to separate it from how the term 'senescence' is typically used in plant physiological literature, where it refers to the beneficial processes of regulated die-back of plant tissues and individual plant parts such as leaves. In particular, we focus on senescence in demographic rates, that is, increases in mortality or decreases in fecundity with age. We use the term 'ageing' to mean growing older and not as an analogous word to senescence. 'Mortality' is the probability that an individual will die at a given age, and 'survivorship' is the cumulative probability of surviving to a given age. Survivorship curves are plots of the number or proportion of surviving individuals over age. If the y-axis is logarithmic, then three different types of curves have traditionally been identified: type I (concave, opening downwards), type II (a straight line) and type III

(convex, opening upwards). For older ages (i.e. disregarding potential changes in mortality over the juvenile period), and assuming that individuals of the same age are identical and in the same constant environment, type I patterns would indicate senescence with an increased mortality with age, type II would indicate a constant mortality with age and type III would indicate a decreasing mortality with age. In natural populations, individual heterogeneity and environmental variation may cause deviations from these patterns, and actual mortality trajectories may not be monotonic (see later), but using this simplistic designation of three types of curves is still a useful way to classify patterns of mortality across species. ‘Fecundity’ is the reproductive output of an individual at a certain age. The demographic rates of mortality and fecundity, and in size-based demography individual growth rate as well, are known as ‘vital rates’. The reproductive value quantifies how much an individual of a certain age is expected to contribute to future population growth and is thus a function of the vital rates, survivorship and fecundity, for future ages. A decrease in reproductive value with age would therefore mean ‘net senescence’, but here we focus on mortality and fecundity independently.

Apart from these demographic terms, we also use some biological terms. Botanists have historically divided plants using several different class systems based on differences in life history. In this text, we usually make a distinction between ‘semelparous’ species (‘monocarpic’ plants, which reproduce at one point in time and then die) and ‘iteroparous’ species (‘polycarpic’ plants, which can reproduce at several points in time). Semelparous plants can be annual, biennial or perennial. Iteroparous species are, by definition, perennial. A third group are annual plants that are not semelparous but have indeterminate growth and are killed off by adverse environmental conditions within a year following germination. Some of these species can behave as iteroparous species and live longer than one year under favourable conditions.

### Scope of This Chapter

In previous studies reviewing demographic evidence for and against senescence in herbaceous plants, it has been concluded that there is some evidence both for and against senescence occurring in non-clonal iteroparous species but no evidence for senescence occurring in primarily clonal species (Pedersen 1999; Roach 1993; Silvertown et al. 2001; Watkinson 1992). We build on the previous reviews and expand these with what has been learned about ageing in recent demographic field studies where ages of plants are known and from theoretical studies. We then discuss these results in relation to evolutionary theories of senescence and to variation in plant traits. We do not include trees and shrubs, except for a few relevant examples. These woody plants may be expected to differ from herbs because the gradual accumulation of dead tissue in woody plants can cause deterioration of vital rates with size for very large, and typically old, individuals (Harper & White 1974). We also do not include studies that use stage-classified matrix projection models to calculate mortality and fecundity trajectories in this review. Such analyses have identified senescence in trees (Baudisch et al. 2013), which may be consistent with the hypothesis that large size can be detrimental for vital

rates of woody plants (Mencuccini et al. 2005). For herbs, mortality typically decreases with size while fecundity typically increases, and we suspect that potential detrimental age effects may not be observed if age-from-stage methods are used. Moreover, without specific age data, the age-versus-size effects cannot be discerned. One of the advantages of using non-clonal herbs to address patterns of senescence is that individual plant age and thus age-dependent patterns are easier to determine and study demographically.

## Age Effects on Mortality

### Semelparous Species

Semelparity can be viewed as an extreme form of senescence. In semelparous species, mortality typically decreases with size, and thus with age, until after reproduction, when death of individuals in a cohort occurs in a very short time period (reviewed in Metcalf et al. 2003). Explanations for the evolution of semelparity in plants focus on trade-offs between life history traits, particularly early and late reproduction (see the discussion of trade-offs later in this chapter). It has been shown that the age of flowering in monocarpic species corresponds to the age, or size, that optimises fecundity given a particular risk of mortality (Young & Augspurger 1991).

### Non-Semelparous Annuals

Several annual plants keep growing and reproducing until they are killed off by adverse environmental conditions, typically after one season. We do not expect the mortality patterns of these species to be interpretable in terms of senescence because it would be hard to separate effects of age from effects of the environment. However, these species are interesting systems for studying senescence in experimental populations with no environmental deterioration. In idealised conditions, when plants can be maintained to ages beyond what which they typically experience in nature, which would be greater than one growing season for annual plants, we would expect to observe traits at late ages that have not been under any selection pressure. However, we are not aware of many such studies (but see one example suggesting that senescence may be present in an annual plant in Roach (1993)). Finally, it should be recognised that species that are annual in some habitats (e.g. with severe winters) may be perennial in others. One example of this is *Poa annua*. Law et al. (1977) studied perennial populations in England and Wales and reported survivorship curves that may indicate senescence in a few populations (Watkinson 1992) as being partly close to linear. However, some of the curves also indicate constant mortality (linear log-survivorship), and the time period was (naturally) short.

### Iteroparous Species Showing No Mortality Senescence

Several decades have passed since plant demographic studies gained popularity among ecologists, and this is reflected in the growing number of published studies from long-

term demographic monitoring projects of perennial plants. Most of these long-term field studies employed size- or stage-based demography to account for population structure, because size is typically a better predictor of mortality and fecundity than age (Caswell 2001). However, age since germination is known for many individuals in these studies, and this information is starting to be used to look at age effects. Many of the studies that have done so have shown no age pattern to mortality. One of the classic studies of several Swedish meadow species (Tamm 1956, 1972a, 1972b), which used marked individuals but of unknown age, suggested constant mortality for nearly all species. Similar patterns were found in other studies using ‘decay curves’, in other words, the loss of marked individuals of unknown age from a population (Antonovics 1972; Sarukhan & Harper 1973).

More detailed long-term studies, in which individuals from different yearly cohorts have been followed through time since establishment and in which ages are thus known for individuals, have shown several different patterns for survival. One early study, by Canfield (1957), with individuals of known ages, reported survivorship data for eleven grass species, where mortality was fairly constant for older individuals, although inspection of the data indicates a weak trend of increased mortality with age in grazed plots and the opposite trend in un-grazed plots. In addition, type II survivorship curves, signifying constant mortality, have been reported for *Poa annua* (Law et al. 1977), and a type III pattern with decreasing mortality with age has been reported for *Viola sororia* (Solbrig et al. 1980). Whereas *P. annua* is very short-lived (often annual), and the observation period covered the entire life span in Law et al. (1977), in the study with *V. sororia* there were no data for individuals near the maximal recorded life span (Solbrig et al. 1980).

Several detailed studies reporting age trajectories of mortality or survivorship have also been published in relatively recent years and are summarised in Table 15.1. Lauenroth and Adler (2008) report constant or decreasing mortality with age in a long-term study of twenty-nine forb and eleven tussock-forming grass species in permanent plots, where survivorship curves were of type II (forbs) and type III (grasses). Judging

**Table 15.1** Studies Published between 1993 and 2014 Describing Genet Mortality Patterns in Herbaceous Perennials over Life Spans

Species	Increase in mortality	Study
19 grasses <sup>a</sup>	No	Chu & Adler 2014
29 forbs and 11 grasses <sup>a</sup>	No	Lauenroth & Adler 2008
<i>Borderea pyrenaica</i>	No	Garcia et al. 2011
<i>Bouteloua gracilis</i>	No	Fair et al. 1999
<i>Gentiana pneumonanthe</i>	No	Rose et al. 1998
<i>Lobularia maritime</i>	Yes	Pico & Retana 2008
<i>Ophrys sphegodes</i>	No	Hutchings 2010
<i>Plantago lanceolata</i>	Yes	Roach et al. 2009

<sup>a</sup> Some populations were the same in these two studies. Whether or not an increase in mortality with age was reported for adult individuals is indicated.

from the data provided in the appendices of these papers, the type III patterns seem to have been driven by decreases in mortality early in life, and there seem to be no trends over age for older ages in either group. However, data for the oldest individuals were scant for most species. From a similar study based in part on some of the same long-term data for nineteen populations of perennial grasses, Chu and Adler (2014) report that mortality decreased with age in all but one population. A lack of evidence of senescence was also reported from a fourteen-year study on *Gentiana pneumonanthe*, in which mortality did not differ between age groups of mature plants (Rose et al. 1998). In addition, vital rates of already established plants did not differ from those of plants established during the study. Also, in a thirty-eight-year mortality data set for genets of the grass *Bouteloua gracilis* there was no effect of age on mortality (Fair et al. 1999). In another very long-term study (thirty-two years) of a large number of individuals of the short-lived orchid *Ophrys sphegodes*, the log-survivorship curve was linear over the plant's life span (Hutchings 2010).

In some species, the anatomy of belowground parts can be used to determine age. Such methods are particularly useful for species with extreme life spans. This method has been used to study senescence of individuals in the very long-lived species *B. pyrenaica*, with life spans of up to 300 years. Senescence was studied in this species using shoot scars on the rhizome to determine plant ages, and five years of demographic data were used to calculate vital rates (Garcia et al. 2011). The results of this study suggested that mortality stayed constant or possibly even decreased with age for old plants. These demographic results are consistent with physiological studies on this species that did not identify any deterioration of plant function with age (Morales et al. 2013; Onate et al. 2012). As in all studies that are primarily cross sectional, the patterns of mortality across different ages must be calculated using the fraction of individuals who survived to those ages (Hadfield 2007), but with these extremely long-lived plant species, longitudinal studies from germination to death are clearly not possible.

### Iteroparous Species Showing Mortality Senescence

Studies with two herbaceous plant species directly support the hypothesis that individuals senesce, and there are a few studies in which indirect results may support this hypothesis (e.g. Tuomi et al. 2013; see also Chapter 16). With the short-lived species *L. maritima*, Pico and Retana (2008) followed 1,367 individuals from three-yearly cohorts and showed a gradually increasing mortality rate with age.

A multiple-cohort long-term study was also done with the herbaceous perennial *P. lanceolata*. In this study, a large number of individuals, nearly 30 000, were planted and followed from establishment to death. These large numbers made it possible to estimate mortality precisely through to the latest ages. Four different cohorts were established over three years; thus, cohort effects could be separated from environmental effects on mortality by having different-aged individuals experiencing the same environment. The results showed that there is a large environmental influence on mortality (Roach 2003), particularly in response to changes in precipitation and temperature.

Moreover, when the environment was favourable, all individuals of different ages showed the same pattern (Roach et al. 2009). However, individuals of older cohorts had higher mortality than younger individuals when mortality was high overall (Roach et al. 2009). Thus, there was an indication of senescence only when conditions were stressful.

Condition-dependent ageing in *P. lanceolata* was also found with respect to growth rate such that older individuals showed negative growth; in other words, they were shrinking, whereas younger individuals had positive growth even during the observed periods of environmental stress (Roach 2012). The advantage of having different-aged individuals, in other words, multiple cohorts, experiencing the same environment in this study was demonstrated when these results were compared to a previous experiment with this same species. A covariate modelling analysis that included both intrinsic variables such as size and reproduction and extrinsic environmental variables such as precipitation and temperature but that only had data for one cohort could not identify any evidence for senescence (Roach & Gampe 2004). These results with *P. lanceolata* are of particular interest because of the detailed data and analyses. Observations of variation across cohorts in demographic patterns also highlight the problems associated with uncovering age-dependent patterns in populations with large environmental influences.

### Conclusions Regarding Empirical Knowledge of Mortality Trajectories

Only a few of the reviewed empirical studies report increases in mortality with age, and it is not clear whether these results reflect the true variability of senescence patterns across plant species. It is interesting to consider both the experimental protocol employed and the variation in the biology of the species studied to understand the variation in these patterns. Firstly, discerning senescence patterns from survivorship curves can be difficult because the functional form of the relationship between age and mortality can change with age (e.g. Dahlgren et al. 2011; Vaupel et al. 2004), and smaller increases in mortality with age for very old individuals can be hard to detect when looking at survivorship curves over all ages. This is particularly true because data for the oldest individuals are scarce in most studies both because few individuals in cohorts reach these ages and because the oldest individuals in most cases have life spans that are longer than the study period (but see Fair et al. 1999; Hutchings 2010). Moreover, the effects of heterogeneity on individual quality may obscure a deterioration with age if the oldest surviving individuals are of a higher quality overall and have a lower mortality (Vaupel & Yashin 1985).

In indeterminately growing species, the effects of size may counteract ageing effects per se as long as individuals are still growing. Size effects therefore can obscure potential negative effects of age (Vaupel et al. 2004) unless they are corrected for. It may also be so that increases in size with age result in an escape from senescence for some period of the life cycle (this is discussed further later). Unfortunately, investigating age and size effects simultaneously has only rarely been done. Moreover, there are reasons to believe that senescence can be difficult to identify in natural populations because environmental effects, well known to affect vital rates, have to be accounted for. Environmental variation

can cause patterns that could mistakenly be assumed to be age effects, for example, if environments of individuals deteriorate over time. In studies not examining multiple cohorts, age and environment cannot be separated in this scenario. Spatial environmental heterogeneity may also make age effects hard to detect. Finally, the studies in which evidence for mortality senescence was found were among the ones where data were available for the entire life spans of the species. This may suggest that a lack of evidence in longer-lived species is due to data limitations and that more data are clearly needed.

### Age Effects on Fecundity

Senescence may, in addition to increased mortality, be manifest demographically as a decrease in fecundity with age. Furthermore, fecundity may be a good biomarker for general physiological decline associated with senescence (Monaghan et al. 2008), and it can be followed within individuals, unlike mortality, to avoid effects of among-individual heterogeneity (Nussey et al. 2008). Fecundity trajectories that have been investigated in long-term monitoring studies of iteroparous herbaceous species show variable results (Table 15.2). In a fourteen-year study on *G. pneumonanthe*, flowering probability did not differ between age groups of mature plants, nor did it differ between plants already established at the start of the study and plants established during the study (Rose et al. 1998). Willems and Dorland (2000) report no relationship between age and flowering probability, flowering number or flowering stem height over a maximum of nine years from the start of flowering for the orchid *Spiranthes spiralis* (average age of flowering was 3.5 years). Using tuber anatomy to determine ages of individuals, Ehlers and Olesen (2004) found that flower number stayed constant with age in old individuals of *Corydalis intermedia*. Perkins et al. (2006) used root anatomy to determine plant ages, for *Potentilla recta* and reported no fecundity senescence. Using similar techniques, Garcia et al. (2011) reported that net reproductive output of both male and female plants increased with age in young *B. pyrenaica* but stayed roughly constant with age for old individuals.

**Table 15.2** Studies Published between 1993 and 2014 Describing Fecundity Patterns in Herbaceous Perennials over Life Spans

Species	Decrease in fecundity	Study
<i>Borderea pyrenaica</i>	No	Garcia et al. 2011
<i>Corydalis intermedia</i>	No	Ehlers & Olesen 2004
<i>Gentiana pneumonanthe</i>	No	Rose et al. 1998
<i>Kosteletzkya pentacarpos</i>	Yes	Pino & Roa 2007
<i>Plantago lanceolata</i>	Yes	Shefferson & Roach 2013
<i>Potentilla recta</i>	No	Perkins et al. 2006
<i>Spiranthes spiralis</i>	No	Willems & Dorland 2000
<i>Trillium grandiflorum</i>	No	Hanzawa & Kalisz 1993

Note: Whether or not a decrease in fecundity with age was reported is indicated.

There are also some studies reporting patterns suggesting fecundity senescence. A few early agronomical studies of grasses report a decrease in fecundity over age (reviewed in Roach 1993). *T. grandiflorum* was found to produce fewer reproductive shoots as individuals aged (Hanzawa & Kalisz 1993). In addition, van Dijk (2009) noted that some traits related to reproduction declined in *Beta vulgaris* as plants came close to the end of their life span. In such cases it may be interesting to determine whether patterns are due to age-dependent senescence or to terminal declines related to time to death.

A recent analysis of the multiple-cohort study with *P. lanceolata* evaluated both age and time-to-death influences on fecundity (Shefferson & Roach 2013). The results showed that fecundity increased, for all cohorts, to a peak at age two and then declined with age. Additionally, the authors showed that there was both an age-dependent and an age-independent decline in fecundity as individuals approached death. Our understanding of reproductive declines with age and terminal reproductive declines as an individual approaches death is still very limited because most studies have not followed individuals for their entire life span. Again, we clearly need more data to understand the breadth of variation in fecundity senescence in herbaceous plants.

### Survival–Fecundity Trade-Offs

The existence of trade-offs between fecundity and plant vitality is a fundamental ecological assumption for which there is much evidence, although within-species trade-offs can often be difficult to detect (e.g. Obeso 2002). For example, observations that non-semelparous annuals produce more seeds per biomass and year than perennials have been attributed to trade-offs between fecundity and life span (Silvertown & Charlesworth 2001). This notion of life history trade-offs is important in the context of senescence if reproduction has a cost in terms of decreased future reproduction and/or increased mortality. Evidence for the effects of trade-offs on senescence patterns has been found in animals (e.g. Good & Tatar 2001), and optimal resource allocation between reproduction and vitality is a major component of theories explaining how senescence evolved (see later).

That reproduction can come at a cost of increased mortality for plants is clearly illustrated in semelparous species. A trade-off between survival and fecundity in these species, related to resource availability, is evident when experimental depression of seed production increases life span (Hautekeete et al. 2002; Noodén 1988). In addition, increased resource availability through fertilisation is reported to have caused iteroparous reproduction in some normally semelparous species (Young & Augspurger 1991).

Fecundity–vitality trade-offs also exist in iteroparous species (Obeso 2002). For example, in *P. annua*, increased reproduction showed a cost in terms of decreased growth and thus decreased future reproduction (Law 1977), and in *Podophyllum peltatum*, reproduction has consequences for the growth pattern of future shoots (Geber et al. 1997). Life history trade-offs can also explain why iteroparous plants commonly show delayed reproduction (Silvertown & Charlesworth 2001). Miller et al. (2012) modelled

expected first flowering time using integral projection models (see also Childs et al. (2003) for monocarps) to show that the average time of first reproduction for a perennial orchid fit these patterns. These survival–fecundity trade-offs shape plant life histories and are likely to affect age trajectories of vital rates. One of the currently unanswered questions is whether survival–fecundity trade-offs change with age in herbaceous species.

## Connections with Theory

### Theories on the Evolution of Senescence and Plants

To understand whether senescence can occur in plants, it is important to compare empirical knowledge to predictions of theoretical evolutionary models. Classical evolutionary theories of senescence are based on the premise that selection will weaken with age (Medawar 1952). The antagonistic pleiotropy theory suggests that mutations giving rise to pleiotropic genes with effects that are beneficial early in life but detrimental late in life can be selected for (Williams 1957). The mutation accumulation theory predicts that a weakening selection pressure over age could also give rise to an accumulation of deleterious late-acting mutations over life (Hamilton 1966). The prediction from these classical theories is that additive genetic variance varies across ages, resulting in a genotype–age interaction. In accordance, a recent study with *Silene latifolia* has demonstrated an increase in the additive genetic variance of traits closely related to fitness (Pujol et al. 2014). The results of this study could not distinguish between mutation accumulation and antagonistic pleiotropy mechanisms, but this quantitative genetic experiment is a first step towards using plants to test these theories. Whereas age-specific demographic patterns can be used to indicate the presence or absence of senescence, these classic theories cannot be directly tested without genetics.

Results from more realistic demographic models challenge the predictions of these classical senescence theories. Observations of indeterminate growth in herbaceous species such as *P. lanceolata* led to new models that have demonstrated that negligible, or even negative, senescence is possible for species that attain a size at reproductive maturity that is less than their maximum size (Vaupel et al. 2004). In addition, a declining selection pressure with age alone may not be sufficient for senescence to evolve in models that take trade-offs and interdependence among vital rates at different ages into account (Wachter et al. 2013; Wensink et al. 2014).

Nevertheless, for species with germ lines that are separated from the somatic cell lineages early in life, the ‘disposable-soma theory’ provides an explanation for how senescence will eventually occur as in this case there exists an age after which an investment of resources in offspring will increase fitness more than an investment in repairing somatic tissue (Kirkwood & Holliday 1979; see also Chapter 2). Models based on the disposable-soma theory have reliably predicted senescence patterns for humans and other mammals, and this theory is how senescence is currently understood to have been favoured by evolution in these species (Kaplan & Robson 2009). However,

a separation of germ cells early in life does not necessarily occur in plants. More general resource-allocation theories still apply, but a larger variation in age patterns is possible (Baudisch & Vaupel 2012). Next, we discuss several features of the biology of plants that may act against the evolution of senescence.

### Unique Biology of Plants that May Cause Deviations from Theory

#### Multiple Meristems

Plants grow from multiple meristems, which are tissues consisting of undifferentiated ‘pluripotent’ stem cells. Even though the main meristems are formed during embryogenesis, new meristems typically can be formed throughout life (e.g. Laskowski et al. 1995; Long & Barton 2000). This implies that a germ cell line is not separated early in life, even in species that are not clonal, and this may be an important difference between plants and higher animals regarding the evolution of senescence (see Chapter 11 for a discussion of modular organisms). Growth from multiple meristems allows plants to be comprised of different modules that can be more or less independent – and even separate in some cases, which would result in clones (see below). Exactly what the proximate physiological causes of senescence would be is beyond the scope of this chapter (but see Chapter 13). Still, the modularity of plants may allow them to possibly cope with ‘stressed’ or damaged modules by ceasing to devote resources to damaged modules (cf. Thomas 2013). In any case, for senescence to occur, all meristems in an individual must deteriorate (e.g. Watson & Riha 2010). Given the diversity of plant growth forms and of plant life spans, the expectation that herbaceous plants will all show the same patterns of senescence does not appear to be realistic.

#### Clonality

Many plants are to some extent clonal; in other words, they can reproduce vegetatively as well as sexually through the production of seeds. Some plants reproduce exclusively vegetatively over at least some parts of their range (one example of this is the primarily Southern European and Western Asian species *Petasites hybridus*, for which female plants are very rare in Northern Europe) (Mossberg & Stenberg 2003). Vegetative propagation can be achieved by the formation of specialised propagules or by fragmentation. Genetic individuals (‘genets’) of clonal species can live for a very long time, sometimes many thousands of years (e.g. Cook 1983), even though there is a turnover of physiological individuals (‘ramets’).

Because of these long life spans, little is known about whether genets of clonal individuals deteriorate with age (e.g. de Witte & Stöcklin 2010), and in fact, the same is true for ramets. A heavy reliance on vegetative propagation may be a life history strategy leading to selection against senescence for the genet because even though clonality in itself may not give species the possibility to avoid senescence, clonal reproduction by separation of modules, leading to the formation of new main meristems, is essentially continuous somatic growth, which has been suggested as a mechanism of how negative senescence may evolve (Vaupel et al. 2004).

Theoretical models have shown that both genets (Gardener & Mangel 1997) and ramets (Orive 1995) may escape senescence in some but not all circumstances depending on their life histories. In these models, clonal reproduction was found to inhibit senescence but not necessarily preclude it if there was also sexual reproduction. Little is known about what actually occurs in nature. However, in one study on a clonal tree, quaking aspen (*Populus tremuloides*), genets were aged based on their genetic diversity and the use of a molecular clock, and a decline in pollen production was found with genet age but not with ramet age (Ally et al. 2010).

Ageing effects in ramets can also be studied in tussock-forming species, even though in this case ramets are typically connected via rhizomes and do not form distinct physiological individuals. In a study of two tussock-forming herbaceous species, in which tussocks were aged based on annual rings in the rhizome, tussock age was positively related to ramet mortality and also to fecundity in one species (Münzbergova et al. 2005). In contrast, studies on grasses (e.g. Lauenroth & Adler 2008) that are also tussock forming suggest decreasing mortality rates with age for genets. In conclusion, there is theoretical and scant empirical evidence both for and against senescence of ramets and genets of clonal plants, but much is still unknown about the effect of clonality on the evolution of senescence.

### Size

Size has traditionally been regarded as better predictor of plant vital rates than age, and plant demographers typically describe populations in terms of size or stage structure rather than age structure (Caswell 2001). However, the relationship between size and demography is not always straightforward and may be confounded by short- or long-term growth patterns of individuals (Shefferson et al. 2014). Moreover, the fact that size, or some correlated measure of vitality, may be more important than age does not mean that there is not also an effect of age (e.g. Lauenroth & Adler 2008). However, if vital rates are mainly size dependent, then senescence may not evolve if size increases with age (Caswell & Salguero-Gómez 2013). This may be particularly true for species that grow continuously with age and thus have higher reproductive output with age. In other words, if an herbaceous species has indeterminate growth for some period of its adult life, then it may escape senescence for that period (Vaupel et al. 2004).

### Sedentariness and Density Dependence

Another feature of plants is that they are sedentary in the sense that established plants are typically permanently attached. This, in combination with density-dependent intra-specific competition, has been suggested to possibly counteract the evolution of senescence (Borges 2009; Seymour & Doncaster 2007). In particular, as density increases, reproductive values of older, larger individuals increase, as does their relative fitness, because younger individuals are out-competed. Selection would then favour high late-life fitness, which could act against the evolution of senescence in populations that typically occur at high densities. However, models showing this pattern assume a stable environment (Seymour & Doncaster 2007), and much is still unknown of how density dependence at different life stages affects plant populations.

### Future Directions

The range of plant life history strategies and growth forms presents a diverse set of models for future studies to understand how trade-offs shape age trajectories of mortality and fecundity. If species are found that do not senesce, this lack of senescence may be due to the existence of multiple meristems, size effects or density dependence. To evaluate these hypotheses, rigorous demographic studies identifying age patterns of demography and physiology will be needed.

### Age Determination

In the majority of the reviewed studies, ages of plants have been known because individuals have been followed from germination. This method of determining ages has a clear advantage in that it is non-destructive. However, it requires long monitoring periods. A few demographic studies have used age rings in roots (e.g. Perkins et al. 2006) and other aspects of plant belowground morphology (e.g. Garcia et al. 2011) to determine ages of herbs. It has recently been shown that for a large number of species it is possible to determine ages of individuals based on root anatomy (Schweingruber & Poschlod 2005). Such methods are likely to become valuable in order to examine patterns of more species, particularly those with long life spans. Determining plant ages in this way will make it possible to take large samples from populations with stable age distributions and use these data to determine mortality trajectories (Dahlgren, Hellmann, Buentgen & Schweingruber, 2016). For extremely long-lived species, molecular techniques such as quantifying genetic diversity in neutral alleles (as used by Ally et al. 2010) may also be possible. Even though simply determining age trajectories for mortality and fecundity will not be sufficient to tell the full story of senescence, as we have shown here, more such studies are needed to determine general patterns.

### Within-Species Studies

There are additional approaches that we believe could prove particularly valuable for learning about senescence in plants. For example, we are aware of no studies that investigate plant senescence in multiple populations of the same species or over environmental gradients within populations. Such studies are needed to determine how age patterns of mortality and fecundity vary within species and to investigate, for example, effects of the environment and within-species genetic variability on these patterns. There are also other questions about environmental gradients; for example, herbs that occupy less nutrient-rich sites are usually more long lived (Nobis & Schweingruber 2013), but whether this is true also within species, and whether it is an effect of less pronounced senescence or of a lower mortality in poorer soils for individuals of all ages, remains to be discovered. Finally, the interactions of environment-by-age and environment-by-genetics-by-age have only minimally been explored (cf. Roach et al. 2009). To address these topics, experimental manipulations in the field will be required.

In the design of future experiments, it is important to recognise that there may be long-term changes in the environment that can influence results. Even in the observational studies of natural populations over time, the length of the study period would have to be several times longer than the life span of the focal individuals if it is to be demonstrated that age patterns are in fact due to age-dependent effects or if the environment (possibly due to intra-specific effects) of different age groups differed.

Temporal trends in vital rates of plants in cyclic environments are illustrative of how age effects could be confounded with environmental change. For example, in a study of *Eryngium cuneifolium*, germination occurred after fire, and with time, the environment deteriorated in the study population (Menges & Quintana-Ascencio 2004). Age effects are therefore not distinguishable from environmental effects in these data. Similar processes, possibly less dramatic, could lead to younger cohorts doing less well than older cohorts because of environmental change. For these reasons, cohort and age effects need to be separated (cf. Roach 2009).

### Among-Species Studies

Comparative demographic studies have already revealed much about the evolution of senescence across the Tree of Life (e.g. Jones et al. 2014) and have been used to study patterns within plants based on calculating age-specific parameters from size data (Baudisch et al. 2013; Horvitz & Tuljapurkar 2008; Silvertown et al. 2001). As more information on how plant vital rates depend on age becomes available, these types of studies will likely be extremely useful for determining general patterns and connections between age effects and traits relating to modularity, traits correlated with life history trade-offs and to the extent growth is determinate (versus indeterminate). As mentioned earlier, plant species are extremely variable in these regards, and among-species studies will likely be valuable to determine the effects. Finally, in the future, when information is obtained from more plant species, it will be particularly informative to do rigorous phylogenetic analyses of senescence patterns.

### Linking Demography and Physiology

In addition to these topics, it is time to go beyond mortality and fecundity and focus on age-specific physiological changes as an additional metric of ageing. Possible physiological metrics of ageing in plants may include age-specific analysis of functional traits such as growth rate and photosynthesis, changes in competitive ability, or changes in oxidative damage and hormone levels with age (see also Chapter 13). This may open up new ways of measuring senescence and provide insights into the mechanisms involved. Combining demographic and physiological approaches can provide stronger evidence for or against senescence, for example, as was done in the cross-sectional study with *B. pyrenaica*, where both types of analyses suggest no deterioration with age (Garcia et al. 2011; Morales et al. 2013; Onate et al. 2012). Physiological measurements in longitudinal studies would be particularly useful to connect physiological and demographic patterns over time and age.

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