LIFE HISTORY TRADEOFFS AND SENESCENCE IN PLANTS

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Abstract

An increasing number of studies have shown that senescence, the functional decline in traits and increased risk of mortality with increasing age, occurs in organisms in wild populations, but there is a wide range of diversity in the patterns of senescence across species. The antagonistic pleiotropy and the disposable soma theories of senescence predict that there will be life history trade-offs between performance at early-and late-life stages. Plants show variation in senescence patterns and thus provide an opportunity to evaluate life history trade-offs and senescence. Many plant species can be easily followed demographically and their environments, resources and allocation to reproduction can be manipulated, which makes them particularly good models to address these theories. I compared the results from 22 studies of plant senescence in the wild and compiled 20 examples of life history trade-offs in plants. Some of the unique features of plants that may influence senescence patterns and trade-offs in the wild are highlighted through the results. I found all three age-specific patterns: age-decline, age-improvement, and no change with age for plants in the wild. The dominant pattern was an age-dependent decline in at least one trait but, even within a species, the age-specific patterns of traits varied. Results also showed that trade-offs vary across environments and that plants can manipulate their resource pool through increases in photosynthesis, which will influence the manifestation of trade-offs. I conclude that aspects of plant biology including dynamic resource pools, the impact of size, dormancy and below ground storage may influence both the patterns of senescence and life history trade-offs. The diversity of plant life forms and life cycles provide a wealth of opportunities to experimentally study senescence in the context of life history trade-offs.

Introduction

Age-dependent declines in performance are predicted to occur in all species because the force of selection on traits is expected to decline with age (Hamilton, 1966). This prediction forms the foundation of the classical evolutionary theories of senescence, yet more recent theoretical work has demonstrated that this prediction may not hold under all circumstances (Baudisch, 2005). Empirical studies in wild populations have evaluated senescence patterns in two ways. First, long-term longitudinal monitoring of individuals, or cross-sectional monitoring of individuals of different ages, have demonstrated age-declines in life history traits, and some physiological traits, in many animal species. Second, meta-analyses of life tables and population trajectories provide smoothed trajectories over age for fertility, mortality and survival to compare species. These meta-analyses, while not as detailed as longitudinal studies that focus on one species, provide valuable information on large scale patterns across species. For instance, Jones et al. (2014) found a wide diversity of age trajectories ranging from declines (senescence) to improvements (no senescence). The diversity of these patterns suggests that senescence may not be 'inevitable' and it calls for a close examination of the life history differences among species that might explain the variation in these trajectories.

Trade-offs among components of life history are predicted by life history theories (Stearns, 1992), and these trade-offs are central to our understanding of senescence. Two senescence theories, the antagonistic pleiotropy, a genetic theory, and the disposable soma theory, a resource allocation theory, both predict that allocation of resources into traits at early-life stages may come at a cost of a decline in later-life performance (Williams 1957, Kirkwood & Rose, 1991). These late-life declines may result in decreased levels of somatic maintenance and increased levels of cellular damage, which is then manifest as a decrease in physiological performance, growth, survival, or reproduction with increasing age. In wild populations, the connection between early- and late-life trade-offs and the patterns of senescence has been established through empirical work with free-ranging vertebrate populations (Lemaître et al., 2015). These studies show that, within a species, individuals that show high allocation to reproduction or growth early in life also have earlier or faster senescence late in life. These trade-offs across traits at different life stages provide support for the disposable soma theory and suggest that if genetic control of these trade-offs is identified then the trade-offs found in vertebrates would also support the antagonistic pleiotropy theory.

To determine the breadth of the connections between life history trade-offs and senescence in wild populations, I did a similar evaluation of the empirical data for plant species. Plants have a number of characteristics that make them good models to study senescence including the fact that, in many species, individuals can be easily marked and followed for their demography. Many species can be experimentally manipulated to change allocation to reproduction and to manipulate resources and environments, which makes them good models to study trade-offs. Moreover, some plants may not senesce because of their higher levels of plasticity, than animals, and their ability to turnover body parts such as leaves and roots and thus discard aged organs in favor of tissues from new, young, growth (Dahlgren & Roach, 2017). A major assumption of the disposable soma theory is that the germ- and soma-tissue lines are separated early in development to protect and ensure the integrity of the germline for future generations (Kirkwood, 1977). Plant and animal senescence had been expected to differ because this developmental segregation of gametes was presumed to occur very late in the development of most plants. Recent empirical and theoretical evidence shows that some plants have a slowly dividing germline that may be functionally equivalent to the early-segregating germline in animals (Lanfear, 2018). Moreover, except for plant species that can live to extreme ages, there is little evidence that plant germlines have increased levels of somatic mutations (Schoen & Schultz 2019). This suggests that trade-offs as predicted by the disposable soma theory should also be predictive of the patterns of senescence in plants.

I evaluated demographic plant senescence studies to determine the patterns of age-dependent change in traits across the lifecycle. Plant senescence may be manifest in a number of different ways, including DNA replication and repair errors (Golubov et al. 2010) or an accumulation of point mutations (Pla et al. 2000), but it is the impact of this somatic damage on demographic traits that is critical. I thus focus on age-changes in mortality, reproduction and physiological traits. I then review the evidence for trade-offs between life history traits and, where possible, connect the results from senescence and trade-off studies with the same, or closely related species. Finally, I propose new questions for research that will move us closer to understanding how and why plant species show a diversity of senescence patterns.

Variation in Plant Senescence

Age trajectories among species and among traits

Both meta-analyses and demographic studies of marked individuals have been used to determine age-dependent change in plant traits. In a meta-analysis of the mortality patterns of 290 angiosperms, Baudisch et al. (2013) showed that 93% of the species evaluated show negligible or even negative senescence, and that this result holds for both short- and long-lived species. In another multispecies analysis of age-dependent mortality of nine tropical trees, Metcalf et al. (2009) showed that early-life mortality is either declining (negative senescence) or displays a plateau (negligible senescence), and some species showed a very high early mortality which decreased sharply and then rose to a plateau when individuals were larger. They also showed that when a cohort consists of primarily very large trees, mortality increases with age and resembles the "bathtub" shape found in human populations (Metcalf et al., 2009). The diversity of aging patterns in plants is clear from these multi-species comparative analyses and similar diversity should be expected from more detailed, single-species, demographic studies.

Our dataset (Figure 1; Table 1) includes published studies with iteroparous perennials that evaluated the performance of individuals of different ages in longitudinal or cross-sectional comparisons. I have added to, and include, studies identified in other recent plant reviews (Munné-Bosch, 2015; Dahlgren & Roach, 2017). I found that only 22 different plant species have been evaluated for age-dependent change in mortality, reproduction or physiological traits. Across traits I found all three patterns of age-specific changes: declines with age; negligible change with age; and increases with age (i.e. negative senescence). Of the species studied, 16 of 22 (75%) showed an age-dependent decline in at least one trait. Reproduction was the most commonly evaluated trait and 11 of 20 (55%) species showed an age decline and only one study showed improved reproduction with age. The other eight species evaluated for reproduction changes with age showed negligible change. There were only ten studies that examined age-changes in mortality and 70% of these showed higher levels of mortality for older individuals, only one species showed decreased mortality with age, and the other two studies showed negligible changes in mortality albeit after some decrease at the earliest ages. Only four studies evaluated age changes in physiological traits. Declines were found in three species, but one of these species *Pinus sylvestris* (Mencuccini, Oñate, Peñuelas, Rico, & Munné-Bosch, 2014) showed declines in some physiological traits but negligible change in other traits. In the other two species, *Cistus clusii* (Munné-Bosch & Lalueza, 2007), and *Plantago lanceolata* (Quarles & Roach, 2019), cross-sectional studies showed that older individuals had lower physiological performance, but for several traits these age-dependent declines were only manifest during stressful conditions. Negligible changes with age were found for physiological traits of *Borderea pyrenaica* (Morales, Oñate, García, & Munné-Bosch, 2013).

Nearly half (10/22) of the senescence studies evaluated more than one trait, and the pattern of senescence across traits was variable. For example, *Silene spaldingii* showed a slight decrease in survival with age, but an increase with age in the number of seed pods and in reproductive value (Tuomi et al., 2013). This increase in reproductive value suggests that the intensity of selection on traits will continue to be high and that senescence has not evolved in this species, despite the decline in survival. All three age-trajectory patterns were found for different traits of the extremely long-lived mountain herb *Borderea pyrenaica* including a decrease with age for the probability of male flowering (when both age and size are considered), no change in age for female flowering or photo-oxidative stress markers, and an increase in survival and reproductive value with age (García, Dahlgren, & Ehrlén, 2011, Morales et al., 2013). The increase in reproductive value with age, and the lack of oxidative declines, is good evidence that the extremely long-lived *B. pyrenaica* does not senesce; but, the contrasting decline in male flowering demonstrates that age-trajectories may not be consistent across traits. Similarly, physiological traits showed variation in age-trajectories in a study on meristem aging in Scots Pine, *Pinus sylvestrus,* where grafted shoots from trees aged 129 to 534 years were compared (Mencuccini et al., 2014). Results showed an increase with age in the percent of total methylated nuclear DNA loci and induction of chemical defenses with meristem age, but otherwise negligible changes with age in growth, reproduction, and hormones. The authors note that without a longitudinal study it is impossible to know whether actuarial senescence occurs in this pine species.

There have been very few detailed demographic studies of closely related species thus the consistency of senescence patterns within groups is not clear. From Table 1, there is limited information to address this question from two species pairs *Cistu*s spp. and *Lemna* spp. Müller, Siles, Cela, and Munné-Bosch (2014) examined flower and seed production in 3-, 8-, and 13-yo *Cistus albidus* plants in experimental plots and found that older plants produced fewer flowers and had higher embryo abortion of mature seeds. Again, there was variation in age-dependent patterns across traits as there was no evidence of a decline in germination capacity with age. In another species, *Cistus clusii*, physiological traits were compared in two age classes and age-declines in lipid peroxidation and PSII efficiency in leaves from the older individuals were found in stressful environments (Munne-Bosch & Lalueza, 2007). They also found age-induced oxidative stress damage in both chloroplasts and mitochondria in newly emerged leaves that had higher amounts of ABA than older individuals. Similarly, consistent age-declines were found in two, closely related, aquatic species *Lemna minor* and *Lemna* *turionifera* (Barks and Laird 2015, Barks, Dempsey, Burg, & Laird, 2018). In both species, age-declines were found for survival, reproduction (production of daughter fronds) and quality of offspring. In the only replicated study with a single species, a longitudinal and a cross-sectional study, in different field sites of *Plantago lanceolata* both showed senescence in reproductive and physiological traits, and survival (Roach, Ridley, & Dudycha, 2009, Shefferson & Roach, 2013, Quarles & Roach, 2019).

Beyond age-trajectories: size and dormancy

In plants, size may obscure age patterns of survival and reproduction (Caswell 2001). Older plants may be larger and their survival may be more size-than age-dependent, but the relative impact of size or age on demography is further complicated by the observation that, shrinkage from a large to a smaller size may improve survival for individuals under stress conditions (Salguero-Goméz & Casper 2010). In the lily, *Trillium grandiflorum*, size and age are positively correlated and reproductive plants are older than non-reproductive individuals (Hanzawa & Kalisz, 1993). But, reproduction in this species occurs after individuals reach a minimum size threshold and size, defined as total leaf area and rhizome volume, is a better predictor of reproductive status in this species that shows negligible change with age in reproduction. A different influence of age and size was found for saltmarsh mallow, *Kosteletzkya pentacarpos,* where size increased fertile shoot production but there were age-effects on adult fecundity that were evident after size effects were accounted for (Pino & de Roa, 2007). Changes in size with age may explain some of the patterns of negligible age-trajectories of traits across plant species (Table 1). *Corydalis intermedia*, a perennial herb in the Poppy family, increases in size with age and flower production increases with leaf area from age 3, when plants start flowering, until around age 11. After this age, the number of flowers remains constant for its remaining lifespan (Ehlers & Olesen, 2004). This species has an underground tuber (storage organ) that keeps increasing in size with age, even for plants at the oldest ages.

Patterns of senescence may also be influenced by other complexities of the plant life cycle including prolonged dormancy, where individuals can remain below-ground in a non-emergent stage. For *Silene spaldingii*, Tuomi et al. (2013) found that dormancy may influence the age-trajectories of vital rates where dormancy can act as a "reboot" to return individuals to a state experienced earlier in life. Mechanistically, it may be that dormancy allows individuals to accumulate limiting nutrients that would otherwise be depleted if the individual emerged (Lesica & Crone 2007). Dormancy may thus retard senescence in some species either due to a reduction of above-ground stress or lower metabolic rates that reduce senescence (Tuomi et al. 2013). Resprouting from dormancy can have both negative (Shefferson et al., 2014) and positive (Gregg & Kery, 2006) effects on survival and reproduction. The effects of dormancy also impact the age-dependent declines in the orchid *Ophrys sphegodes* where an increase is found in reproduction and survival for several years before these vital rates level off and become age-independent (Hutchings 2010). Older individuals spend a greater proportion of their lives in dormant, non-flowering, condition suggesting long life might be a consequence of less regular emergence and flowering, which may reinvigorate the plant and enable flowering when an individual does reemerge. This 30-year orchid study showed that despite the fact that older plants flower after emergence from dormancy, and there is thus no age-decline in the probability of flowering, the older plants have reduced vigor manifest as smaller flowering spikes, and possibly fewer flowers in spikes and fewer rosette leaves. Additionally, with respect to life history trade-offs, frequent flowering reduces lifespan but the rejuvenation from longer than average dormant periods enables flowering to follow emergence at any age (Hutchings, 2010).

Life History Trade-offs

Resource allocation and acquisition

There is clear evidence for trade-offs among closely related species (Gadgil & Solbrig, 1972, Stearns, 1992, Roff, 2002), but our understanding of within species is less clear. Most importantly, at the level of individuals within populations, trade-offs will depend on variation in resource acquisition and allocation among individuals (Noordwijk & de Jong, 1986). There has been a particular interest in the trade-offs associated with the costs of reproduction (for plants see Obeso, 2002). The studies I retrieved (Table 2), show negative correlations between early- and late-life history traits. Of the 20 species, 9 (45%) show trade-offs between reproduction and survival, and 15 (75%) show a trade-off between early- and late-reproduction. In plants, the costs of reproduction are typically assessed by experimentally preventing or reducing fruit set, or by increasing reproductive allocation with supplemental hand-pollination. Nearly half of the studies were experimental manipulations. In young Mediterranean Aleppo pine trees (*Pinus halepensis*), for example, the experimental removal of developing female cones resulted in increased cones one year later (Santos-del-Blanco & Climent, 2014). This is a rare example of a cost of reproduction in a forest tree that has been demonstrated by a manipulative experiment.

Covariation between life history traits will be influenced by a resource acquisition-allocation balance (Noordwijk & de Jong, 1986). In plants, trade-offs due to resource allocation to reproduction may not be manifest if resource acquisition is increased prior to or during reproduction. For example, in dioecious plant species females generally show a higher cost of reproduction than males, but a study with *Silene latifolia*, found that females unexpectedly showed more vegetative growth than males after the onset of reproduction (Delph & Meagher, 1995). The authors hypothesized that either there were other unmeasured trade-offs, or the lower trade-off between reproduction and growth in females may have been due to increases in the resource pool for females, via increases in photosynthesis, in response to increases in resource demand during flowering. If a reproducing individual can increase its resource acquisition, then reproductive costs may not be observed unless resources are very low (Tuomi et al., 1983). A variable resource pool is particularly likely in plants, not only because resources may be increased through increases in photosynthesis, but also because plants can reallocate or resorb nutrients among functions and plant structures (Ashman, 1994). These compensation mechanisms, that increase the size of the resource pool for individuals, will yield weaker correlations than expected by the disposable soma theory that assumes that resources are limited (see Tuomi et al., 1983).

Beyond resources: environmental and size influences on life history trade-offs

Environmental variation influences resource acquisition and the expression of trade-offs (Obeso, 2002). Environmental effects on trade-offs in plants have been shown in a number of studies and vary among closely related species. Ågren & Willson (1994) evaluated the cost of seed production in two *Geranium* species, by excising stigmas to prevent seed set, and found trade-offs between manipulated seed set and the probability of flowering the following year in two *G. sylvaticum* populations, but not in *G. maculatum* populations. They hypothesized that these differences may be due to differences in the length of the growing season. Similarly, in studies with two long-lived orchids *Dactylorhiza lapponica* and *Gymnadenia conopsea,* experimental increases in fruit production also resulted in differences in reproduction-survival trade-offs across populations that differed in the length of their growing season and summer temperatures (Sletvold & Agren 2015a).

Even within a species, across environments, life history trade-offs can vary. With *Plantago coronopus*, a short-lived perennial herb, Villellas & García (2018) found both negative and positive correlations among vital rates in 11 populations across the species' range. Their results showed that correlations between reproduction and survival varied with environmental stress and were negative in populations with low soil fertility, but the correlation between these traits was positive in locations with abundant soil resources. Similarly, increased allocation to reproduction in *Lychnis flos-cuculi* reduced fecundity the next year in less fertile sites but there was no cost to increased reproduction in more fertile sites (Biere, 1995). Variable life history trade-offs under other environmental conditions have also been found in other studies (e.g. Sandvik, 2001), and some of the impact of these environmental effects may be via changes in resource acquisition and compensation across environments (Tuomi et al., 1983). In stressful environments, where individuals of small size are at higher risk, the trade-off between reproduction and survival may be indirectly mediated by size, where resources directed to reproduction reduce the growth rate, and possibly cause shrinkage in size, and then smaller sized individuals have a higher risk of mortality (Miller et al., 2012).

Connecting senescence and life history trade-offs

There are only a few plant species for which we know both the pattern of senescence and patterns of life history trade-offs, and there are two species that show results consistent with the predictions of the disposable soma theory. The aquatic plant *Lemna turionifera* shows a trade-off between fecundity and lifespan as well as senescence in mortality and reproduction (Barks et al., 2018). Additionally, several studies with the orchid *Dactylorhiza lapponica* show trade-offs among vital rates and a clear pattern of senescence that is consistent with the disposable soma theory. First, with respect to trade-offs, a study with *D. lapponica* at inland and coastal sites (Sletvold & Ågren, 2015b) showed survival-reproduction trade-offs only at the short-season inland site, but growth-reproduction trade-offs, and trade-offs with reproduction the following year, were found at both sites. The variation in some of these life history trade-offs with length of the growing season is consistent with the hypothesis that there is a plasticity to the resource pools for plants, and longer, warmer growing seasons, should allow individuals to accumulate more resources and thus minimize the competition between traits that require resources (Sletvold & Ågren, 2015b). In a second study, experimental increases and reductions in fruit production of *D. lapponica* showed that the costs of reproduction and the shape of the trade-off function differed across sites and that this was consistent with variation in resource availability and the timing of resource allocation to different traits at the different sites (Sletvold & Ågren, 2015a). Actuarial senescence has also been identified in *D. lapponica* from a 32-year data set and the pattern of senescence varied across environments (Dahlgren et al., 2016). Dahlgren et al. (2016) also found additional support for a trade-off between survival and reproduction in this species and interestingly, these costs of reproduction were observed without experimental manipulations (see Ehrlen & van Groenendael, 2001). Together the results of these studies are not only consistent with the disposable soma hypothesis, but they also add interesting insight into the question about whether an early segregated germline is critical for senescence (Lanfear, 2018), because *D. lapponica* is a tuberous orchid for which all above-ground biomass dies back at the end of the growing season and a new replacement tuber and below-ground shoot bud grows.

Variation in the patterns of age-dependent declines (Table 1) provides unique opportunities to evaluate life history trade-offs for species that do not show senescence. The perennial orchid *Spiranthes spiralis* shows no evidence of senescence in mortality or reproduction, but this species does show a trade-off between reproduction and growth/maintenance (Willems & Dorland, 2000). Similarly, after an early-life increase in reproduction, the orchid *Ophrys sphegodes*, shows negligible senescence in reproduction and survival, but a trade-off between flowering frequency and lifespan (Hutchings, 2010). Showing a different pattern, there are two species that showed negligible senescence and no trade-offs. The first, *Gentiana pneumonanthe*, a long-lived perennial that overwinters below ground or produces overwintering shoots, shows age-independent mortality and reproduction and no cost of reproduction (Rose, Clarke, & Chapman, 1998). Similarly, *Corydalis intermedia*, shows no trade-off between reproduction and vegetative growth, and a constant number of flowers after age 11 (Ehlers and Olsen, 2004). Given the plasticity of life history trade-offs across environments, it is difficult to discern whether trade-offs in these latter examples would be found if the studies had been done in more resource-limited environments.

Conclusions and future directions

Despite the fact that there have been relatively few studies on plant senescence in wild populations, and that most of these studies have been done with herbaceous perennials, it is clear that plant species provide a wealth of opportunities to explore the diversity of aging (Salguero-Gómez, Shefferson, & Hutchings, 2013). The variation in plant age-specific changes, that includes declines, negligible and even improvements in trait performance with age, is an excellent platform to test our theories of aging such as the disposable soma and antagonistic pleiotropy theory. The studies discussed here show many different patterns of the relationship between senescence trajectories and life history trade-offs including: trade-offs and senescent decline, trade-offs but no senescent decline, and no trade-offs and no senescent decline in traits. Plasticity in resource pools, either due to variation in environments or to compensation mechanisms (see Section 3.1), will mean that trade-offs in life history traits may not always be found. The disposable soma theory assumes that individuals have limited resources that can be allocated to somatic maintenance or reproduction and the impact of dynamic resource pools may violate this assumption. Another assumption of this theory is that the germline is segregated early in development. The timing of this segregation is currently an open question (Lanfear 2018), and new approaches to study cell fate in plants are expected to clarify this issue (Schoen & Schultz 2019). Research in this area is in a nascent stage and the studies that have been done raise new questions for future studies such as: How do size and age interact to determine trait trajectories and trade-offs? Does variation in resource pools and life cycle dynamics require revisions to our current senescence theories? And, what are other gaps in our ability to connect life history trade-offs to patterns of senescence in plants?

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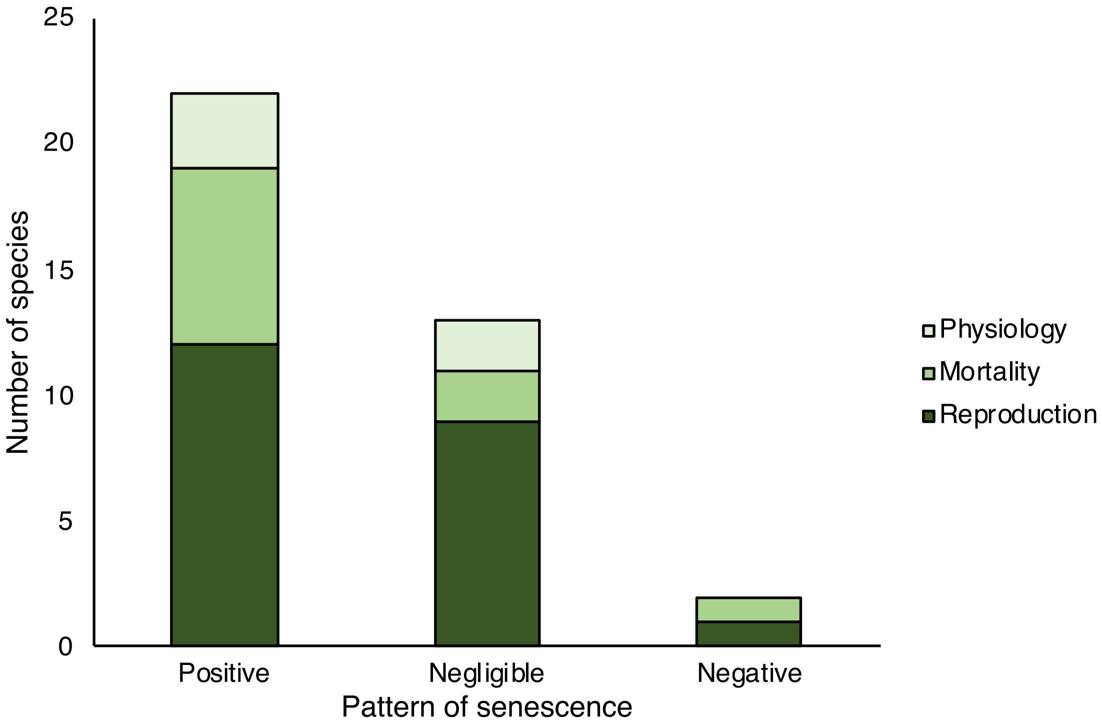

Figure 1. Patterns of plant senescence found in published studies of iteroparous perennials that have evaluated reproduction, survival, or physiology of different ages.

Table 1. Studies of age-dependent changes in mortality (M), reproduction (R), and/or physiology (P) in plants. Positive, negligible, or negative, senescence denotes studies that found decreases, no change, or increases, in trait performance with age respectively; the methods, cross-sectional (C) or longitudinal (L), are noted.

						Senescence Pattern			
Species	Family	Length of study	Median lifespan†	Sample size	Method	Positive	Negligible	Negative	Study
Lobularia maritima	Brassicaceae	4	3	1367	L	M	-	-	Picó & Retana (2008)
Silene latifolia	Caryophyllaceae	3	3	283	L	R	-	-	Pujol *et al*. (2014)
Silene spaldingii		25	(25)	76	L	M		R	Tuomi *et al*. (2013)
Cistus albidus	Cistaceae	1	15	24	C	R	R	-	Müller *et al*. (2014)
Cistus clusii		1	15-20	32	C	P	-	-	Munné-Bosch & Lalueza (2007)
Carex secalina	Cyperaceae	4	4	100	L	R	-	-	Bogdanowicz et al. (2011)

Borderea pyrenaica	Dioscoreaceae	5	(300)	748	C	R (males)	R, P	M	García et al. (2011); Morales et al. (2013)
Astagalus scaphoides	Fabaceae	25	21	515	L	M, R	-	-	Tuomi et al. (2013)
Gentiana pneumonanthe	Gentianaceae	14	14	501	L	-	M, R	-	Rose et al. (1998)
Lemna minor	Lemnaceae	1		216	L	M, R	-	-	Barks & Laird (2015)
Lemna turionifera		1		560	L	M, R	-	-	Barks et al. (2018)
Trillium grandiflorum	Liliaceae	1	18	202	C	-	R	-	Hanzawa & Kalisz (1993)
Kosteletzkya pentacarpos	Malvaceae	9	8	1225	L	R	-	-	Pino & de Roa (2007)
Dactylorhiza lapponica	Orchidaceae	32	4	2184	L	M	-	-	Dahlgren et al. (2016)
Ophrys sphegodes		32	4.5	2000	L	-	M, R	-	Hutchings (1987 and 2010)
Spiranthes spiralis		17	6	120	L	-	R	-	Willems & Dorland (2000)

Corydalis intermedia	Papaveraceae	1	6	4904	C	-	R	-	Ehlers & Olesen (2004)
Pinus sylvestrus	Pinaceae	15	750	49	C	P	P, R	-	Mencuccini et al. (2014)
Plantago lanceolata	Plantaginaceae	10	3	30000	L	M, R	-	-	Roach et al. (2009), Shefferson & Roach (2013)
		1	3	200	C	M, R, P	-	-	Quarles & Roach (2018)
Elymus excelsus	Poaceae	2	5	279	C	R	-	-	Li, Li, & Yang (2018)
Potentilla recta	Rosaceae	1	5	279	C	-	R	-	Perkins et al. (2006)
Populus tremuloides	Salicaceae	1		5000	C	R	-	-	Ally et al. (2010)

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†Maximum lifespan is given in parentheses for species for which median lifespan is not available.

Table 2. Plant studies showing phenotypic trade-offs between early traits and late-life reproduction or survival (* denotes experimental manipulation; all species are herbaceous except the tree species marked with †).

Species	Family	Trade-off	Study
Beta v. maritima	Amaranthaceae	Reproduction and survival	Hautekèete et al. (2001)
Astrocaryum mexicanum	Arecaceae	Early-reproduction and late-reproduction/survival	Piñero et al. (1982)
Senecio keniodendron	Asteraceae	Early reproduction and late reproduction/survival	Smith & Young (1982)
Podophyllum peltatum	Berberidaceae	Early-reproduction and late-reproduction/survival	Sohn & Policansky (1977)
Alnus viridis ssp. crispa	Betulaceae	Early reproductive effort and late reproduction*	Houle (2001)
Silene latifolia	Caryophyllaceae	Early-reproduction and late-size/reproduction*	Delph & Meagher (1995)
Geranium sylvaticum	Geraniaceae	Early-late reproduction*	Ågren & Willson (1994)

Gladiolus sp.	Iridaceae	Early-reproduction and survival	Rameau & Gouyon (1991)
Sidalcea oregana ssp. spicata	Malvaceae	Early- and late- reproduction	Ashman (1994)
Metrosideros polymorpha †	Myrtaceae	Fast growth and survival	Morrison & Stacy (2014)
Aspasia principissa	Orchidaceae	Early reproductive effort and late reproduction*	Zimmerman & Aide (1989)
Cypripedium calceolus		Growth and future reproduction	Shefferson et al. (2003)
Dactylorhiza lapponica		Reproduction and survival	Dahlgren et al. (2016)
		Early-reproduction and late growth/ reproduction/survival*	Sletvold and Ågren (2015b)
Epidendrum ciliare		Early-late reproduction*	Ackerman & Montalvo (1990)

Gymnadenia conopsea		Early-reproduction and growth/late reproduction or survival*	Sletvold and Ågren (2011)
Plantago coronopus	Plantaginaceae	Early-growth/reproduction and late reproduction/survival	Villellas & García (2018)
Poa annua	Poaceae	Reproduction and survival	Law (1979)
Pinus halepensis †	Pinaceae	Early-and later-reproduction*	Santos-del-Blanco & Climent (2014)
Ranunculus acris	Ranunculaceae	Early and late reproduction	Hemborg (1998)
Siparuna grandiflora	Siparunaceae	Early and late reproduction	Nicotra (1999)