Letters

Senescence, ageing and death of the whole plant: morphological prerequisites and constraints of plant immortality

Introduction

Recently, there has been a new wave of interest in plant senescence (Salguero-Gomez *et al.*, 2013; Thomas, 2013; Jones *et al.*, 2014; Lee & Muzika, 2014). Plant life cycles have several characteristics that are seldom paralleled in animals, including life-long existence of undifferentiated tissues and a modular body plan allowing abandonment of old parts (García *et al.*, 2011; Thomas, 2013). Plants, especially herbs, are famous for rarely showing senescence, that is, fitness decreasing with age (Munne-Bosch, 2008). However, to assess the extent to which it does occur, and identify factors related to it is often hindered by lack of information about plant longevity (Ehrlén & Lehtila, 2002; Schweingruber & Poschlod, 2005; de Witte & Stoecklin, 2010; but see Nobis & Schweingruber, 2013).

Despite the view of plants as being in a continuous state of renewing and replacing of modules (see Fig. 1), allowing continuous whole-plant rejuvenation (Thomas, 2013), the relationship between module senescence and whole-plant senescence remains largely unexplored (Salguero-Gomez *et al.*, 2013). Organ, module and whole-plant senescence were recently examined in a comprehensive review by Thomas (2013). According to the author, plants have adopted three strategies to avoid senescence: (1) escaping it by replacing old modules (i.e. clonal plants); (2) resisting it by having durable organs (in the case of trees); and (3) pre-empting it by undergoing programmed death after flowering and fruiting (monocarpic herbs).

Although this classification is useful and relevant, we wish to address the question of whether these categories really represent strategies of plants to avoid senescence. In particular, we wish to examine an alternative view in which these categories correspond to common morphological constraints. We support our reasoning using large morphological and herbchronological datasets of European herbaceous species (Klimešová & de Bello, 2009; *c.* 2700 species from Central Europe in the CLO-PLA database; Nobis & Schweingruber, 2013: *c.* 500 species from Switzerland) as an example of a temperate flora. Finally, we propose a list of critical morphological characters deserving consideration in further studies of plant ageing and senescence. First, however, it is important to define the relevant terms. In this paper, we use the term ‘ageing’ as synonymous with ‘increasing in age’ without respect to plant fitness, and use ‘senescence’ to mean decreasing fitness with increasing age.

Building the plant body

To evaluate potential morphological constraints on plant immortality it is necessary to understand how the plant body is constructed. The plant body is composed of one or several shoots; typically each shoot reiterates the same species-specific architecture, position and timing and has a similar lifespan (Serebryakova, 1977; Hallé *et al.*, 1978). However, shoots differ in their origin, as they can arise as primary shoots, axillary shoots or adventitious shoots depending on the buds (meristems) from which they are sprouting.

The primary shoot is formed on the shoot pole of the embryo as a product of the shoot apical meristem (SAM; Fig. 1). The SAM, sometimes called the ‘fountain of youth’ (Baurle & Laux, 2003), produces repeated modular structures consisting of stem segments bearing leaves and daughter (axillary) meristems (IU; Fig. 1). The primary shoot is the only shoot for the majority of annual and biennial herbs, monopodial palms, cycases and ferns. In monocarpic plants, the SAM finally turns into a generative structure, and the plant dies after fruiting (Fig. 2-1).

Axillary meristems (AMs; Fig. 1), which are direct descendants of the apical meristem of the primary shoot, are sources of apical meristems for axillary shoots that yield first, second, etc. orders of plant branching and form the bodies of the majority of perennial plants.

In some plants, however, the axillary meristems are complemented by adventitious meristems (AdMs; Fig. 1). In the case of adventitious meristem formation, new shoots are produced independently of the SAM of the primary shoot, arising instead from differentiated cells of the hypocotyl and/or roots (Fig. 1) or to a lesser extent from leaves (Kerstetter & Hake, 1997). Independent formation of adventitious meristems by dedifferentiation of already differentiated tissue might protect a plant from mutations occurring in primary and/or axillary meristems, and it can also provide meristems when all stem parts (with all their SAMs and AMs) are lost to damage or are undeveloped (e.g. in mycoheterotrophs, Klimešová, 2007). Such adventitious meristems are produced by *c.* 8% of the temperate flora (Klimešová & de Bello, 2009), but individual species differ vastly in their abilities to form adventitious meristems and shoots and also in the roles that adventitious shoots play in their lives (Rauh, 1937; Fig. 2-5).

Programmed death vs perenniality

Thomas (2013) considered the transition of the shoot apical meristem into the generative stage and its consumption by flower formation (meristem determinacy) to be the factor limiting further plant growth and the signal for senescence in monocarpic plants. In this view, perenniality is due to the existence of indeterminate (neither generative nor dormant) meristems on the plant body during flowering and fruiting (Thomas, 2013). However, examination of comparative data for the temperate flora shows that indeterminate meristems occur after flowering in only about half of the herbaceous perennials (Klimešová & de Bello, 2009). These meristems are found in plants that exhibit monopodial growth (see Fig. 2-2), or that have sympodial growth with overlapping shoot generations (Bell, 1991), (see Fig. 2-3, 2-4). However, sympodially growing plants with nonoverlapping shoot generations (another half of perennial herbs) have no indeterminate meristems present on the plant body during and immediately after flowering, similarly to monocarpic herbs. Therefore, the nonexistence of indeterminate meristems on a plant body is not a universal prerequisite for programmed death of monocarpic plants. Given the great flexibility of meristem activation and/or cell dedifferentiation, programmed death cannot be linked with any single trait of plant functional morphology. Instead, it is better viewed as evolutionarily arising many times due to selective effects of external sources of mortality. When plants are subjected to lethal disturbance or stress in a juvenile, pre-reproductive phase, it is beneficial for the surviving individuals to invest in further survival and repeated reproduction and therefore employ the polycarpic life history strategy. For species inhabiting habitats which cause lethal damage or stress to adult, reproductive plants, it is beneficial to invest all the resources in one reproductive event and therefore employ the monocarpic life history strategy (Gadgil & Bossert, 1970; Stearns, 1992). In herbs of temperate regions, the major morphological differences between these two strategies is that the polycarpic species have overwintering organs that store carbon and they also position resting buds out of the reach of frost, that is, in soil or near its surface (Raunkiaer, 1907; Otzen, 1977).

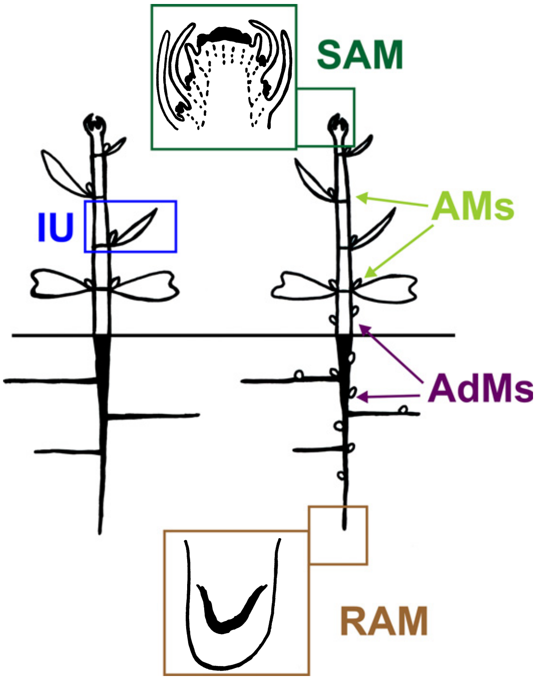

Fig. 1 Basic architectural units in angiosperms are shown for eudicot seedlings. Left plant, without adventitious meristems; right plant, with adventitious meristems on roots and hypocotyl. Diagram shows locations of shoot apical meristem (SAM), root apical meristem (RAM), axillary meristems (AMs) and adventitious meristems (AdMs). IU indicates the plant module, that is, the smallest iterated unit of shoot.

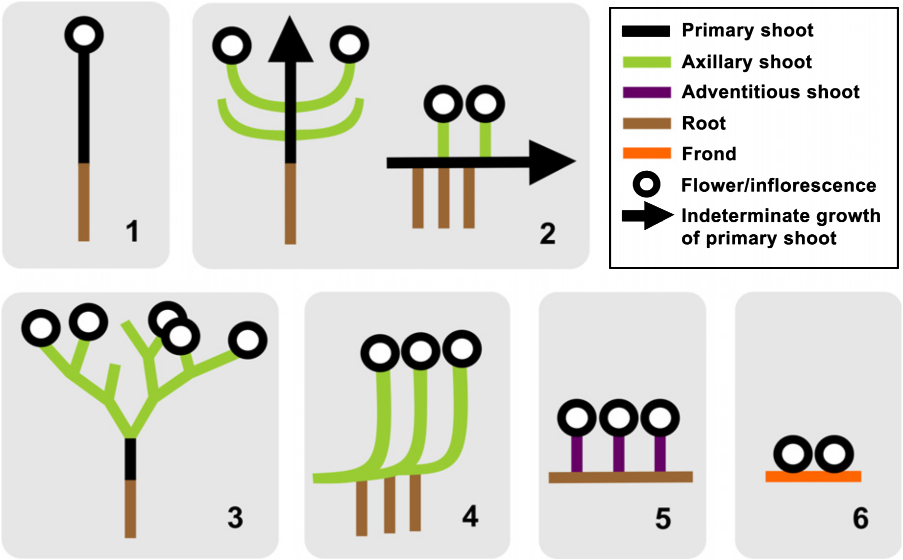

Fig. 2 Angiosperm architecture classified by representation of three types of shoots in the adult plant body. 1, Plants with only the primary shoot for the whole lifespan, for example, some annuals and monopodial palms; 2, plants with both primary and axillary shoots, with the primary shoot growing for the plant's entire life, for example, monopodial trees and herbs; 3, plants with both primary and axillary shoots, the primary shoot being part of the body but its growth not lasting the plant's entire life, for example, sympodial trees and perennial nonclonal herbs; 4, plants with axillary shoots only, for example, clonal rhizomatous and stoloniferous herbs; 5, plants with adventitious shoots only; 6, plants with reduced body (e.g. pondweed frond).

Resisting by durable organs vs organ replacement

In addition to the flexibility of meristem formation there is great variability in the persistence of different types of shoots during the plant lifespan (see overview in Fig. 2). Whereas nearly all plants start their growth as tiny seedlings consisting of the primary shoot, only some of them retain all or part of this shoot over their whole plant lifespan (Fig. 2-1, 2-2, 2-3). Indeed, all clonal plants eventually replace the primary shoot with axillary and/or adventitious shoots (Fig. 2-4, 2-5).

Thomas (2013) contrasts the durability of tree organs of with organ replacement of clonal herbs. However, although clonal growth is much more frequently found in herbs than in trees (clonal herbs are three times more common than nonclonal herbs whereas clonal trees are much rarer than nonclonal trees in the temperate flora; Aarssen, 2008; Klimešová & de Bello, 2009), in both trees and herbs, some species can replace their organs while others cannot (Fig. 2). The plants that cannot replace them are dependent on key organs such as the primary shoot (i.e. trunk) in the case of nonclonal trees and the main (primary) root and base of the primary shoot in nonclonal herbs. These two growth forms differ only in the timescale over which organ replacement can take place: months in herbs and decades in trees (Klimešová & de Bello, 2009).

The inability to replace perennial organs, considered in light of the necessity for their continued functioning, constitutes a clear morphological constraint, which we suggest limits the lifespan of many perennial herbs and trees rather than promoting it. Although senescence signs are not commonly reported from the field (Baudisch *et al.*, 2013; but see Roach *et al.*, 2009; Ally *et al.*, 2010), fitness declining with ageing has been noticed in pot experiments and botanical gardens, where intraspecific competition is reduced (Lukasiewicz, 1962; J. Martínková, unpublished). The old individuals of herbaceous species in such conditions can be distinguished by decay of the oldest parts of the main root, resulting in disintegration of the plant individual and inability to move reserve meristems belowground to protect them over the winter (Ignatiyeva, 1965).

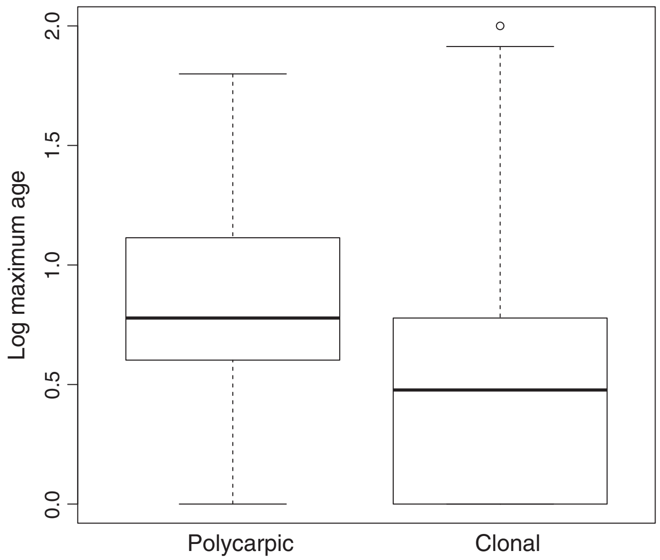

Fig. 3 Comparison of maximum plant ages (determined by growth-ring counting; see Nobis & Schweingruber, 2013, for details) between nonclonal polycarpic and clonal plants (distinction between clonal and nonclonal plant came from CLO-PLA database, Klimešová & de Bello, 2009). The difference explains 11.0% variation in log maximum age and is highly significant using analysis of variance (ANOVA) ($P < 0.001$; df = 1, 313). The difference between clonal and polycarpic plants remains significant using phylogenetic regression assuming Brownian motion evolution ($R^2 = 2.2\%$, $N = 305$; using the pgls function from the caper package in R (http://www.R-project.org); Orme, 2012; and using DaPhnE phylogeny from Durka & Michalski, 2012).

The lifespan of the oldest plant parts in clonal as well as nonclonal herbs varies considerably, and is longer for nonclonal species (Fig. 3). This difference suggests that there is a close link between clonality and longevity (as suggested by Thomas, 2013). However, this link can be interpreted in two opposing ways: (1) clonal herbs are those that are not able to ensure comparable durability of plant organs to nonclonal herbs, with clonality thus an

Table 1 Phylogenetic conservatism of traits related to plant lifespan

Trait	Number of absences	Number of presences	Estimated *D*	Confidence interval of *D*	Test of difference from Brownian motion evolution	Test of difference from random trait distribution (no phylogenetic signal)
Eudicot herbs only						
Annual lifespan	704	263	0.479	[0.355 to 0.605]	< 0.001	< 0.001
Monocarpic	885	82	0.483	[0.242 to 0.727]	< 0.001	< 0.001
Capacity for clonal growth	593	374	0.423	[0.319 to 0.531]	< 0.001	< 0.001
Root sprouting capacity	816	151	0.652	[0.482 to 0.832]	< 0.001	< 0.001
Presence of taproot	384	581	0.376	[0.271 to 0.483]	< 0.001	< 0.001
All eudicots						
Root sprouting capacity	879	202	0.531	[0.386 to 0.676]	< 0.001	< 0.001
Woodiness	1024	82	−0.394	[−0.548 to −0.228]	0.981	< 0.001

Phylogenetic conservatism is assessed using Fritz & Purvis's (2010) *D* statistic, which is appropriate for discrete traits. A value of unity indicates complete absence of phylogenetic signal in the trait, that is, complete phylogenetic randomness. A zero value indicates phylogenetic conservatism corresponding to Brownian motion evolution (i.e. slow, random evolution of the trait value along the phylogenetic tree). Negative values indicate strong phylogenetic conservatism. Confidence intervals for *D* were calculated assuming binomial distributions of number of character trait transitions on the given tree. Only eudicots were analysed, as perennial monocotyledonous plants are always potentially clonal in the temperate zone and never possess taproots.

escape from the constraint of low primary shoot durability; or (2) clonality might have provided plants a way to reduce longevity of plant organs under a selective regime that favours short organ lifespans.

Evolutionary conservatism and ecological drivers of morphological constraints on plant longevity

Individual morphological traits related to plant lifespan show fairly different degrees of phylogenetic conservatism (Table 1). Capacity to form adventitious buds is least conserved, but many other traits relevant to ageing (e.g. clonality, annual life span) show much lower degrees of conservatism than, for example, woody habit. This means that they have evolved independently in response to ecological forces that selected for particular survival strategies.

In monocotyledonous plants, clonality is an apomorphic character of the whole clade, whereas persistent perennial organs (tree trunk and herb primary root) are found only in dicotyledonous plants, namely in herbs and trees in the temperate zone. In eudicots, woodiness is an ancient character, with clonality and monocarpic life history appearing later (Mogie & Hutchings, 1990). The ability to form adventitious buds is a recent innovation that has appeared many times in dicotyledonous herbs and thus shows low phylogenetic conservatism (see also Rauh, 1937). Interestingly, although forming adventitious meristems is an evolutionarily variable character usually responsible for clonal growth of dicotyledonous trees (Del Tredici, 2001), its role in preventing manifestation of senescence (genetic and other effects, see e.g. Brutovská *et al.*, 2013) due to meristem ageing is not known. For example, aspen, forming clones of considerable age, generates new trunks by adventitious sprouting from roots rather than from apical meristems (Mitton & Grant, 1996); it is known to show signs of senescence only over very long timescales (Ally *et al.*, 2010).

Conclusion

We revisited the three strategies identified by Thomas (2013) to avoid senescence (clonality, durability of organs and programmed death) and propose considering them as traits of functional morphology that are involved in adult plant body formation and potentially relevant to effects of plant ageing. As an additional morphological character not mentioned by Thomas (2013) we propose adventitious shoot formation. However, it has not been determined whether these morphological characters represent constraints or adaptations to plant ageing. We believe that by considering the role of morphology in plant growth and maintenance and conducting comparative studies of age-related phenomena across various morphological types we can gain a better understanding of the relationships between plant ageing and these phenomena.

Acknowledgements

The authors are indebted to F. H. Schweingruber for providing data for and valuable comments on a previous version of the manuscript, to A. Bartušková for figures and to J. Rosenthal for language editing. This study was funded by the Czech Science Foundation (project no. 14-36079G, Centre of Excellence PLADIAS) and by the Academy of Science of the Czech Republic (RVO 67985939).

Jitka Klimešová[1]*, Michael Peter Nobis[2] and Tomáš Herben[3,4]

[1]Institute of Botany, Academy of Sciences of the Czech Republic,
379 82 Třeboň, Czech Republic;
[2]Swiss Federal Research Institute WSL, Birmensdorf,
Zürcherstrasse 111, 8903 Birmensdorf, Switzerland;
[3]Institute of Botany, Academy of Science of the Czech Republic,
CZ-252 43 Průhonice, Czech Republic;
[4]Department of Botany, Faculty of Science, Charles University,
Benátská 2, 128 01 Praha 2, Czech Republic
(*Author for correspondence: tel +420 384 721 156;
email klimesova@butbn.cas.cz)

References

Aarssen LW. 2008. Death without sex – the 'problem of the small' and selection for reproductive economy in flowering plants. *Evolutionary Ecology* **22**: 279–298.

Ally D, Ritland K, Otto SP. 2010. Aging in a long-lived clonal tree. *PloS Biology* **8**: e1000454.

Baudisch A, Salguero-Gomez R, Jones OR, Wrycza T, Mbeau-Ache C, Franco M. 2013. The pace and shape of senescence in angiosperms. *Journal of Ecology* **101**: 596–606.

Baurle I, Laux T. 2003. Apical meristems: the plant's fountain of youth. *BioEssays* **25**: 961–970.

Bell AD. 1991. *Plant form.* Oxford, UK: Oxford University Press.

Brutovská E, Sámelová A, Dušička J, Mičieta K. 2013. Ageing of trees: application of general ageing theories. *Ageing Research Reviews* **12**: 855–866.

Del Tredici P. 2001. Sprouting in temperate trees: a morphological and ecological review. *Botanical Review* **67**: 121–140.

Durka W, Michalski SG. 2012. DaPhnE: a dated phylogeny of a large European flora for phylogenetically informed ecological analyses. *Ecology* **93**: 2297.

Ehrlén J, Lehtila K. 2002. How perennial are perennial plants? *Oikos* **98**: 308–322.

Fritz SA, Purvis A. 2010. Phylogenetic diversity does not capture body size variation at risk in the world's mammals. *Proceedings of the Royal Society B: Biological Sciences* **277**: 2435–2441.

Gadgil M, Bossert WH. 1970. Life historical consequences of natural selection. *American Naturalist* **104**: 1–24.

García MB, Dahlgren JP, Ehrlén J. 2011. No evidence of senescence in a 300-year-old mountain herb. *Journal of Ecology* **99**: 1424–1430.

Hallé F, Oldeman RAA, Tomlinson PB. 1978. *Tropical trees and forests: an architectural analysis.* Berlin, Germany: Springer Verlag.

Ignatiyeva IP. 1965. On the problem of the life-cycle in the tap-root and fibrous-root polycarpic herbaceous plants. *Botaniceskiy Zhurnal* **50**: 903–916 [In Russian].

Jones OR, Scheuerlein A, Salguero-Gomez R, Camarda CG, Schaible R, Casper BB, Dahlgren JP, Ehrlen J, Garcia MB, Menges ES *et al.* 2014. Diversity of ageing across the tree of life. *Nature* **505**: 169–173.

Kerstetter RA, Hake S. 1997. Shoot meristem formation in vegetative development. *Plant Cell* **9**: 1001–1010.

Klimešová J. 2007. Root-sprouting in myco-heterotrophic plants: prepackaged symbioses or overcoming meristem limitation? *New Phytologist* **173**: 8–10.

Klimešová J, de Bello F. 2009. CLO-PLA: the database of clonal and bud bank traits of Central European flora. *Journal of Vegetation Science* **20**: 511–516.

Lee CA, Muzika R-M. 2014. Plant senescence for ecologists: precision in concept, scale, and terminology. *Plant Ecology.* doi: 10.1007/s11258-014-0398-8.

Lukasiewicz A. 1962. Morphologic development types of perennials (Morfologizno-rozwojowe typy bylin). *The Poznan Society of Friends of Science. Department of Mathematical and Natural Sciences, Biology* **27**: 1–398 [In Polish].

Mitton JB, Grant MC. 1996. Genetic variation and the natural history of quaking aspen. *BioScience* **46**: 25–31.

Mogie M, Hutchings MJ. 1990. Phylogeny, ontogeny and clonal growth in vascular plants. In: van Groenendael J, de Kroon H, eds. *Clonal growth in plants: regulation and function.* The Hague, the Netherlands: SPB Academic Publishing, 3–22.

Munne-Bosch S. 2008. Do perennials really senesce? *Trends in Plant Science* **13**: 216–220.

Nobis MP, Schweingruber FH. 2013. Adult age of vascular plant species along an elevational land-use and climate gradient. *Ecography* **36**: 1076–1085.

Orme D. 2012. *The caper package: comparative analysis of phylogenetics and evolution in R.* Vienna, Austria: R Foundation for Statistical Computing.

Otzen D. 1977. Life forms of three *Senecio* species in relation to accumulation and utilization of non-stuctural carbohydrates. *Acta Botanica Neerlandica* **26**: 401–409.

Rauh W. 1937. Die Bildung von Hypocotyl- und Wurzelsprossen und ihre Bedeutung für die Wuchsformen der Pflanzen. *Acta Nova Leopoldina* **4**: 395–555.

Raunkiaer C. 1907. *Planterigets Livsformer og deres Betydning for Geografien.* Copenhagen, Denmark: Munskgaard.

Roach DA, Ridley CE, Dudycha JL. 2009. Longitudinal analysis of *Plantago*: age-by-environment interactions reveal aging. *Ecology* **90**: 1427–1433.

Salguero-Gomez R, Shefferson RP, Hutchings MJ. 2013. Plants do not count.. or do they? New perspectives on the universality of senescence. *Journal of Ecology* **101**: 545–554.

Schweingruber FH, Poschlod P. 2005. Growth rings in herbs and shrubs: life span, age determination and stem anatomy. *Forest Snow and Landscape Research* **79**: 195–415.

Serebryakova TI. 1977. On the main "Architectural Models" of herbaceous perennial plants and modes of their transformation. *Bjulleten Moskovskogo Obshchestva Ispytateley Prirody, Otdel biologicheskiy* **82**: 112–128 [In Russian].

Stearns SC. 1992. *The evolution of life histories.* London, UK: Oxford University Press.

Thomas H. 2013. Senescence, ageing and death of the whole plant. *New Phytologist* **197**: 696–711.

de Witte L, Stoecklin J. 2010. Longevity of clonal plants: why it matters and how to measure it. *Annals of Botany* **106**: 859–870.

Key words: adventitious meristem, axillary meristem, clonal plant, main root, plant ageing, plant senescence, tissue turnover.