



Hypothesis: Plant stem cells hold the key to extreme longevity

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ABSTRACT

Theories of ageing explain how multicellular organisms age by means of an immortal germ line and a perishable soma, whereby accumulated damage is preferentially distributed to the soma. Plants do not clearly separate germline and somatic cells, which questions whether current theories of ageing are applicable to plants. Plant stem cells have germline-like features, while plant tissue that dies in a mostly seasonal manner, such as leaves and xylem, have soma-like properties. Plant stem cells may therefore hold the key to understanding how plants can reach extreme ages and we discuss model systems that may be suitable to advance the field of plant ageing.

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The multifaceted disposition of ageing has been puzzling scientists for decades. It is mostly centred on the notion of why natural selection has allowed this death-associated deleterious trait to remain in our life history. In the late nineteenth century August Weismann first proposed a theory to explain ageing in the context of a perishable soma and an immortal germ line, where the soma represents the 'body' which carries the reproductive germline [1]. The theory suggested that somatic vulnerability exists as a death mechanism to rid the population of frail individuals [2,3]. Building on Weismann's initial idea, Thomas Kirkwood proposed the disposable soma theory to explain that ageing happens due to a lack of a selective pressure for somatic maintenance [4]. According to the resource allocation principle [5], due to the direct contribution of the germline to the individuals' fitness, energy invested in it takes precedence over maintenance of the soma. The optimal level of somatic repair is often lower than what is required to fix all the damage, hence inevitably leading to somatic ageing [3]. In fact, a perishable soma may be required to maintain an immortal germline and Sheldrake [6] reasoned that irreparable damage could only be removed from the population by means of asymmetric cell division whereby immortal daughter cells renew at the cost of perishable mother cells that acquire the damage. These theories demand a clear distinction between germline and soma and

indeed, this is crucial for the development of most multicellular organisms [7]. However, such distinction is not well defined in plants since reproduction occurs after the transition of the apical meristem from a vegetative to reproductive state. While very few animals can live past a hundred years, plants are known for their extreme longevity with the bristlecone pines of at least several thousand years old [8]. Therefore, one key question that remains is: how does the lack of germline-soma separation influence ageing in plants?

Plant stem cells hold the key to plants' extraordinary lifespan. Unlike most animals [9], plants have a continuous supply of stem cells located in the root and shoot meristems (Fig. 1) [10–12]. These cells give rise to new organs that allows them to persist through extreme conditions. Stem cells are continuously maintained through self-renewal mechanisms occurring within stem cell niches or dedifferentiation of adult structures (Fig. 1) [13–15]. This ongoing supply of highly pluripotent stem cells responsible for tissue homeostasis, repair and post-embryonic growth can give rise to new organs or complete plants: we surmise that those cells function akin to a germline and may hold the key to extreme longevity in plants.

Theories of ageing predict that in order to maintain immortal stem cells, the plant needs soma-like cells to absorb irreparable damage. Differences in plants' life cycles and the presence of indeterminate meristems can provide further explanations on plants' remarkable longevity in some species. Like animals, plants adopt either a semelparous or an iteroparous lifestyle. Semelparous (monocarpic) species are short-lived, as commonly seen in annual

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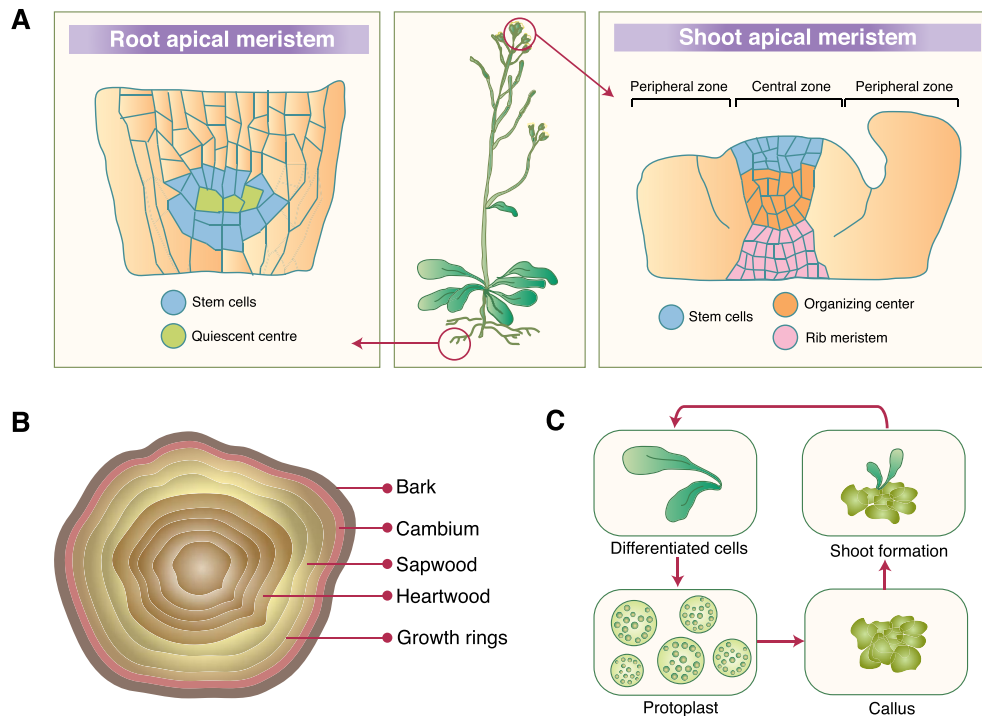


Fig. 1. Plant stem cells. (A) Schematic diagram of longitudinal sections of shoot apical meristem and root apical meristem in Arabidopsis. Stem cells are organised within the stem cell niche where adjacent cells serve to maintain their pluripotency. Adapted from Gaillochet and Lohmann [31]. (B) Cross section of a tree trunk. Cambium cell division results in wood and bark formation but can also induce lateral root or shoot formation. Wood and bark consist of cells that have undergone programmed cell death. Largely seasonal plant growth leads to the emergence of growth rings. (C) In plants, adult structures can dedifferentiate to become cells with stem cell-like properties. Plant mesophyll cells, stripped from their cell walls by enzymatic digestion, are called protoplasts and can dedifferentiate into pluripotent cells. Treatment of protoplasts with the phytohormones cytokinin and auxin promotes cell proliferation and callus formation. Roots and shoots can regenerate from the callus to yield an adult plant.

and biennial plants. This life history is characterized by a single reproductive event followed by decline in fitness and death soon after. While vegetative shoot apices were initially indeterminate, they soon become determinate floral apices causing monocarpic plants to senesce after reproduction and seed dispersal [16,17]. Any irreparable damage can therefore be removed from the population as part of whole plant senescence.

On the contrary, perennials, consisting of clonal and non-clonal members, adopt another reproductive strategy known as polycarpy or iteroparity. Many perennial species are long-lived. Woody perennials could bypass senescence at the individual or whole-organism level. This may be due to the fact that the apical meristem of at least one of the perennial's shoot axes remains indeterminate throughout its lifespan [18]. Furthermore, the cambium, also known as the undifferentiated lateral meristem, is capable of continuous cell division similar to embryonic stem cells while damages may be taken up by differentiated vascular tissues that undergo programmed cell death [6]. Thus, perennials have ample opportunity to remove accumulated damage through asymmetric cell division and subsequent death of soma-like cells. In fact, much of the plant dies in a seasonal fashion, through leaf senescence and wood and bark-formation. One could consider long-lived woody perennials such as the bristlecone pine, coast redwood and common yew as amalgamations of short-lived somas that can be discarded when damaged without having much impact on the whole individual.

Additionally, perennials that undergo clonal growth may employ a different survival strategy [16,19]. Vegetative growth of clonal plants occurs through the formation of sprouts, coppice shoots and root suckers [20]. The individual clones or genets of these perennials are collectively made up of physiological units known as ramets. Some clonal plants appear to live forever and a

seagrass (*Posidonia oceanica*) clone was estimated at a minimum age of between of 80,000 and 200,000 years old [21]. Individual ramets undergo senescence and the continuous production of new ramets is needed to prevent genet senescence. Often, the rate of ramet production far exceeds the rate of ramet death, overall contributing to the non-ageing phenotype typically observed in clonally reproducing perennials.

Answers to the question on 'how do long-lived plants avoid ageing' could be achieved by investigating molecular and cellular differences between stem and somatic cells of meristems from long-lived and short-lived plants. Using high-throughput sequencing approaches, a recent study has demonstrated that the shoot meristem in an oak tree aged over 200 years old is protected from the accumulation of deleterious mutations [22]. Although large trees have more opportunities to amass harmful mutations arising from DNA replication errors [19,23], the authors conclude that mutations from replication errors are less significant than those induced by environmental factors such as ultraviolet radiation [22]. While no evidence for duplication of DNA repair genes is observed in the oak genome, the oak meristem is physically protected from ultraviolet mutagenesis as it is located in buds surrounded by leaf-like structures. Additional studies on other tree species may inform whether the low frequency of fixed somatic mutations is prevalent among all long-lived perennials. There is also much to learn from multicellular algae such as the volvocine algae [24,25]. This family of green algae that reproduces asexually have a complete germline-soma differentiation. Asymmetrical cell division during embryogenesis marks the first step of the germline-soma separation and analyses of cellular differences between the two cell types may discover how damage is selectively moved to the soma. Interestingly, unicellular and multicellular volvocine algae species exist and the evolution of germline-soma division of

labour is a hallmark of multicellularity [26]. Finally, the study of somatic embryogenesis [27,28] may highlight how damage is removed from somatic cells. Somatic cells may accumulate a disproportionate amount of damage and asymmetric distribution of accumulated damage may occur during early somatic cell division. An attractive model system could be regeneration of plants from mesophyll protoplasts [29] as a cell type that is exposed and possibly likely to accumulate damage. Protoplasts from *Arabidopsis* mesophyll cells can be induced to regenerate plants [30], allowing the myriad of molecular and genetic toolsets available for this model plant to be utilised.

Somatic ageing is a universal phenomenon in life and similarities exist in the fundamental processes of ageing between plants and other multicellular organisms. Hence, theories of ageing that have been developed for non-plant organisms may yield additional insights into plant senescence. Long-lived trees, volvocine algae and somatic embryogenesis may represent important model systems for answering fundamental questions on somatic ageing. We hope that the above stimulates further discussion in the field of plant ageing and we believe that, because of the extreme ages that some plants can achieve, plant research will likely benefit all ageing research.

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