

## PLANT SENESCENCE

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### Summary

Senescence is a terminal stage of plant development. It often, but not invariably, ends in the death of cells, tissues, organs or the whole plant. At the cell level there are a number of different senescence pathways, most of which are autolytic, that is, the genetic and biochemical events originate within the senescing cell itself. Nucleus, vacuole, plastids

and mitochondria interact during cell senescence. Up to the point where organelle integrity is lost, some kinds of senescence may be halted, extended or even reversed by various treatments, but beyond this threshold there is a rapid decline in viability leading to death. Developmental cell senescence and death occur during differentiation of xylem, floral tissues, embryos and seeds. Leaves, fruits and some flowers lose chlorophyll during senescence as chloroplasts differentiate into pigmented plastids. The products of chlorophyll breakdown are deposited in the cell vacuole. Proteins and nucleic acids are hydrolysed and the nitrogen and phosphorus liberated are exported from the leaf to sink tissues. Fruit ripening shares a number of regulatory and biochemical features with leaf and flower senescence. Senescence contributes to root turnover, an important factor in global carbon balance. Plants and their parts often must attain maturity before they are able to respond to signals that induce senescence. Floral induction and seed formation stimulate senescence. In monocarpic species the entire plant undergoes reproductive death. Polycarpic plants flower repeatedly during their lifetimes, and show no clear relationship between senescence and longevity. Senescence is a strategic and tactical response to seasonal and unpredictable stresses, including changing daylength, flooding, drought, excessive light, darkness, nutrient limitation and disease. The timing of senescence in relation to carbon capture and nutrient remobilization is a major determinant of crop yield. Senescence and related processes account for significant postharvest losses and food wastage.

## 1. What is Plant Senescence?

### 1.1. Terminology

#### 1.1.1. Senescence

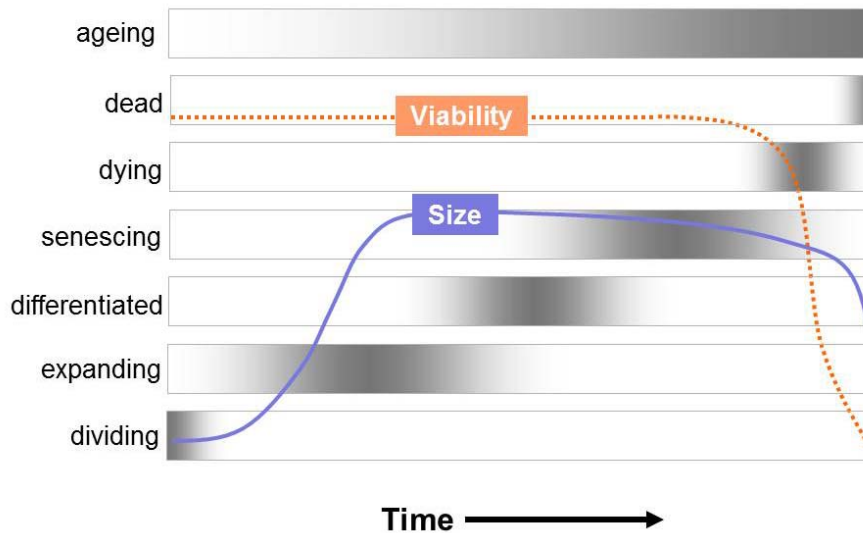


Figure 1. Senescence and related events in the life-history of a plant and its parts. The sequence of events is reiterated at all levels in the hierarchy of plant organization, from cells, tissues, and organs through to individual plants, communities, and even whole floras. Note that ageing includes, but is not limited or defined by, terminal senescence and death phases.

Senescence, which is part of a cloud of terms referring generally to the process or condition of growing old, has a specialized meaning in plant biology (Figure 1). A *Thesaurus* search for 'senescence' reveals words for maturity, ripeness, seniority and longevity, but the dominant associations are with notions of decay, decline, gerontology, morbidity and mortality. This reflects the etymological origin of the word (from Latin *senescere* to grow old) and its association with senility and the medical problems of human ageing.

Current physiological understanding of the senescence condition and its positive roles in plant growth, differentiation, adaptation, survival and reproduction, supports a definition that acknowledges senescence to be a phase of development that follows the completion of growth, is absolutely dependent on cell viability and which may or may not be succeeded by death.

### **1.1.2. Ageing**

Ageing (sometimes also spelled 'aging') is another term, like senescence, that has become associated with deterioration. In the general biological context, however, it should be considered to refer to changes that occur with time, and therefore to embrace the time-based processes of growth and differentiation as well as maturity and senescence.

### **1.1.3. Death**

Death is a condition or state and is the culmination of, and separate from, the process of dying. The philosopher Ludwig Wittgenstein wrote "Death is not an event in life". Application of the term 'cell death' to the physiology of senescence, though widespread, seems inappropriate. By definition, changes that occur in dead cells are post-mortem and non-biological. Biologists studying terminal events in development need to distinguish between the regulated activity of viable biological structures and the pathological outcomes of organic collapse.

### **1.1.4. Program**

The expressions 'senescence program' and 'programmed cell death' are extensively used. The idea of a program as applied to living systems has been taken from computer science. The purposeful nature of a particular biological process, such as senescence, is conceived to be the consequence of control by the equivalent of an executable machine routine: hormones and other signal molecules, kinases and transcription factors are activated in sequence, leading to physiological change. Senescence, like many events in the plant lifecycle, proceeds according to a timetable determined by developmental and environmental factors and mediated by a genetic program.

## **1.2. Relationship between Senescence and Development**

Development is the general term for the changes in form brought about through growth and differentiation. Because post-mitotic expansion processes in plants are largely driven by water, growth is not necessarily associated with increase in dry mass.

Differentiation is the change in structure and function that results in cell, tissue and organ specialization. The capacity to reverse the process of differentiation is a characteristic of the plastic nature of plant development. Senescence and development interact at different levels. Senescence is part of the program that specifies cell fate. It is triggered differentially in tissues and organs, resulting in complex anatomies and morphologies that change and adapt over time. It is the means by which resources are recycled from obsolete body parts to new developing structures. Finally variations on the senescence program theme have been shaped by evolution to give rise to a diversity of structures within the angiosperm lifecycle.

### 1.3. Relationship between Senescence and Ageing

As discussed in Section 1.1.2, the changes with time that fall under the general term ageing are not necessarily deteriorative, although in the long run errors will accumulate and living tissues will show signs of wear and tear. According to some proposed models, senescence is an accelerated form of ageing. Senescing organs, tissues and cells are built either to fail quickly or to be deficient in the mechanisms that otherwise defend against physiological decline. A related view is that, since ageing and eventual death are thermodynamically unavoidable, senescence has evolved as a developmental strategy that pre-empts the inevitable, enabling the individual plant to control its own viability and integrity over the course of the lifecycle. This is sometimes called the Samurai Law of Biology ('it is better to die than to be wrong'). Such is the current state of knowledge that it is difficult to resolve the interconnections between ageing and senescence mechanisms, and they will continue to be fascinating areas of research and speculation.

### 1.4. Relationship between Senescence and Death

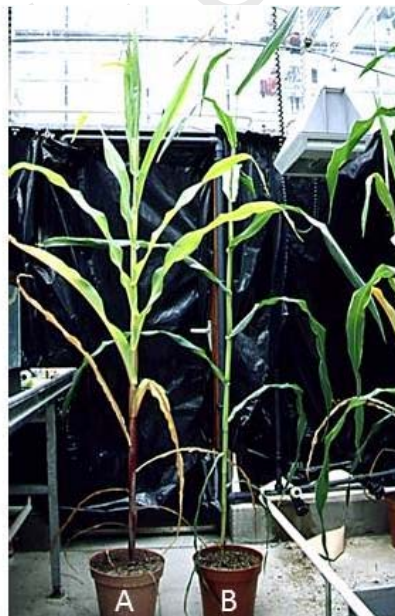


Figure 2. Leaf senescence in maize (*Zea mays*). The plant on the left (A) is growing on low levels of nitrogen fertilizer and shows the typical gradient of yellowing within and between leaves. The plant on the right (B) has been genetically modified to reduce expression of a gene encoding an enzyme of nitrogen mobilization in senescence.

Senescence and death differ fundamentally: by definition, senescing tissue is viable, dead tissue is not. There is a transitional condition between the two states during which metabolism modulates into abiotic chemistry. This terminal period is often rapid and always irreversible. The preceding senescence phase is usually comparatively extended. Cell membranes and organelles remain intact, and organs stay turgid. In some cases, notably the senescence of green (mesophyll) cells in leaves, this phase is reversible until almost all of the cells' macromolecules have been recycled and exported to the rest of the plant. Cells within the same organ can be at different stages in the progression from senescence to death. For example there is a gradient of cell age from leaf base to tip in grass species such as maize (*Zea mays*; Figure 2). Senescence proceeds from the tip downward, and towards the veins from interveinal regions of the lamina. This heterogeneity within a single structure can make it difficult to disentangle senescence-phase, terminal and post-mortem events.

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### Biographical sketch

**Howard Thomas** is Emeritus Professor of Biological, Environmental and Rural Sciences at Aberystwyth University, Wales, UK. He has held visiting professorships at Universities in Switzerland and the United States. His research interests include investigation and modification of cellular, biochemical and evolutionary mechanisms of plant senescence and death, with special emphasis on pigment and protein metabolism. Approaches include cloning, mapping and exploiting genes determining senescence, late-season and post-harvest deterioration, food, feed and bioprocessing quality and consumer perception in a range of crop and amenity species. He has been active in the application of imaging and machine-learning methods for non-destructive analysis of plant development and gene flow, and remote field to landscape-level monitoring of crops and ecosystems. He also has a special interest in the cultural significance of scientific research and promotion of links between science and the arts.