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Some Aspects of Leaf Senescence

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1. Introduction

The word *senescence* derives from two Latin words: *senex* and *senescere*. *Senex* means 'old'; this Latin root is shared by 'senile', 'senior', and even 'senate'. In ancient Rome the 'Senatus' was a 'council of elders' that was composed of the heads of patrician families. *Senescere* means 'to grow old'. The Merriam-Webster online dictionary defines *senescence* as 'the state of being old or the process of becoming old'. Aging is also the process of getting older. Therefore, aging has been regarded as a synonym of senescence, and the two words have often been used interchangeably, which, in some cases, is fine but in some other cases causes confusion. This paper will first briefly discuss the terminology of senescence, and then will review the literature related to mitotic senescence, a topic that has not been well discussed in the plant senescence research area and discuss some results relating to nutrient remobilization during leaf senescence.

2. Terminology and types of senescence

Senescence is a universal phenomenon in living organisms, and the word *senescence* has been used by scientists working on a variety of systems, such as yeast, fruit fly, worm, human being and plants. However, the meaning of the word *senescence* to scientists working on different organisms can be different, and the difference can be subtle in some cases and very obvious in some other cases.

3. Plants exhibit mitotic senescence, post mitotic senescence and cell quiescence

Plants exhibit both types of senescence. An example of mitotic senescence in plants is the arrest of apical meristem; the meristem consists of non differentiated, germ line-like cells that can divide finite times to produce cells that will be then differentiated to form new organs such as leaves and flowers. The arrest of apical meristem is also called proliferative senescence in plant literature .This is similar to replicative senescence in yeast and animal

cells in culture. Another example of mitotic senescence is the arrest of mitotic cell division at early stages of fruit development. Fruit size is a function of cell number, cell size and intercellular space, and cell number is the major factor.

Cell number is determined at the very early stage of fruit development and remains unchanged thereafter. Post mitotic senescence occurs in some plant organs, such as leaves and floral petals. Once formed, cells in these organs rarely undergo cell division; their growth is mainly contributed by cell expansion; thus, their senescence, unlike mitotic senescence, is not due to an inability to divide. This type of senescence involving predominantly somatic tissues is very similar to that.

4. Physiological regulation

Reproductive development appears to play an important role in regulating proliferative senescence in plants, which is especially true in many monocarpic plants. Hensel *et al.* (1994) found that meristems of all inflorescence branches in the wild-type *Arabidopsis* ecotype Landsberg *erecta* (L*er*) ceased to produce flowers coordinately, but such a coordinated proliferative arrest did not occur in the wild-type L*er* plants with their fruits surgically removed. Similarly, meristem arrest was not observed in a male-sterile line that never sets seeds. This result suggests that the arrest of inflorescence meristems is regulated by developing fruits/seeds (Hensel *et al.*, 1994). Hensel *et al.* further proposed two models to explain the effect of developing fruits on the mitotic activity of meristems. One model is that a factor necessary for sustaining mitotic activity at the SAM is gradually taken and eventually depleted by developing fruits, resulting in arrest. The other model is that developing fruits produce a negative regulator of mitotic activities and that the negative regulator is transferred to and accumulated in the SAM to a threshold level so that the SAM is arrested. The factor, either positive or negative, is unknown.

5. Nutrient remobilization during leaf senescence

Senescence is the last stage in the development of leaves and other plant organs. While many plants are perennial (barring adverse conditions leading to premature death), and some species even very long-lived (at least from a human perspective), senescence and death of organs such as leaves is often an annual event. Due to its importance for agriculture, the senescence of annual crops (e.g. corn, rice, wheat, barley and some legumes) has been most intensely studied (Feller & Fischer, 1994; Hayati *et al.*, 1995; Crafts-Brandner *et al.*, 1998; Yang *et al.*, 2003; Robson *et al.*, 2004; Parrott *et al.*, 2005;Weng *et al.*, 2005). Additionally, as in other areas of plant science research,*Arabidopsis* has emerged as an important model system (Diaz *et al.*, 2005; Levey & Wingler, 2005; Otegui *et al.*, 2005). These plants show monocarpic senescence, i.e. fruit set and maturation are directly associated with whole-plant senescence and death. Other types of senescence, such as top senescence (in species with bulbs, tubers, tap roots or rhizomes), deciduous senescence (in some trees and shrubs of temperate climate zones) and progressive senescence (e.g. in evergreen trees) have received less attention. In contrast to annuals, leaf (or whole-shoot) senescence is often not directly associated with seed filling in perennial plants (Feller & Fischer 1994; Nood´en *et al.*, 2004). However, nutrient

remobilization from senescing plant parts to surviving structures is a hallmark of the 'execution' of the senescence process in both annual plants, in which nutrients are retranslocated to the seeds, and perennial species, in which nutrients are transported to surviving structures such as bulbs and roots.

Plants need a number of elements in higher quantities or concentrations to complete their life cycle (macronutrients, including C, O, H, N, P, S, K, Mg and Ca), while a number of additional elements (micronutrients, including Fe, Mn, Zn, Cu, B, Mo, Cl and Ni) are needed in comparatively small quantities (Marschner, 1995). Some elements are essential only for specific taxonomic groups (e.g. Na, Si) and/or are considered beneficial (Marschner, 1995).

5.1 Nitrogen remobilization

Quantitatively, nitrogen is the most important mineral nutrient in plants (Marschner, 1995). It is often a limiting factor for plant growth, yield and/or quality (Gastal & Lemaire, 2002; Good *et al.*, 2004). Additionally, as for carbon, the principal form in which many plants acquire nitrogen from the environment (nitrate) is more oxidized than the form in which it can be integrated into metabolites and macro molecules, demanding substantial energy input for the synthesis of nitrogen compounds. Although the biochemistry involved is different, the establishment and maintenance of a symbiosis with N2-fixing microorganisms (e.g. in legumes) is also costly (Crawford *et al.*, 2000; Lodwig & Poole, 2003). For these reasons, efficient N remobilization increases the competitiveness of wild plants. Additionally, due to the economic and ecological (N runoff from agricultural soils) cost of N fertilization, this trait is of considerable importance to farmers.

In most plant tissues, the largest fraction of organic nitrogen, which is potentially available for remobilization during senescence, is contained in proteins. In photosynthetically active tissues of C3 species, over 50% of this nitrogen is found in soluble (Calvin cycle) and insoluble (thylakoid) chloroplast proteins (Peoples and Dalling, 1988; Feller and Fischer, 1994). Intriguingly, ribulose-1,5-bisphosphate carboxylase/ oxygenase (Rubisco) alone represents 50% of the total plastidial nitrogen.

All other cellular nitrogen fractions, including cytosolic and other proteins, nucleic acids, chlorophylls and free amino acids, while not negligible, represent relatively minor stores of organic nitrogen. Efforts at understanding nitrogen remobilization during leaf senescence have therefore focused on the biochemistry of plastidial protein degradation. Mae *et al.* (1983), using elegant 15 N-labeling techniques, have demonstrated that the synthesis and degradation phases of Rubisco are surprisingly clearly separated during leaf development. High rates of synthesis were observed until full leaf expansion; after this point, synthesis was minimal, but degradation rates started to increase. In this context, it is well known that the photosynthetic capacity of a leaf declines early during leaf senescence, while mitochondrial integrity and respiration are maintained longer (Gepstein, 1988; Feller and Fischer, 1994). That efficient N remobilization is associated with (early) loss of CO2 assimilation represents a formidable problem in annual crops. In this context, agronomists are well aware of the negative correlation between seed protein and yield.

5.2 Macro- and micronutrient remobilization

Developing (young) leaves constitute significant net importers ('sinks') for all nutrients, which are utilized to build the organ's cellular and molecular components. After the so-called sink–source transition (Ishimaru *et al.*, 2004; Jeong *et al.*, 2004), leaves become net exporters ('sources') of carbohydrates from photosynthesis, while import (through the xylem) and export (through the phloem) of phloem-mobile nutrients are (roughly) at an equilibrium in mature leaves (Marschner, 1995). The onset of leaf senescence is associated with a transition to net export of 'mobile' (see below) compounds, i.e. total (per leaf) content of some nutrients starts to decrease (Marschner, 1995). The literature often refers to this situation as 'redistribution', 'retranslocation', 'resorption' or 'remobilization' (Marschner, 1995; Killingbeck, 2004).

The main transport route from senescing leaves to nutrient sinks is the phloem (Atkins, 2000; Tilsner *et al.*, 2005). Using various approaches, including sampling and analysis of phloem sap and (radioactive) tracer studies, it has been established that macronutrients with the exception of calcium (i.e. N, P, S, K and Mg) are generally highly mobile in the phloem, while micronutrients with the exception of manganese (i.e. Fe, Zn, Cu, B, Mo, Cl and Ni) show at least moderate mobility (Marschner, 1995). As a consequence, while some mobile nutrients decrease during leaf senescence, this is not true for calcium, which continues to accumulate throughout a leaf's life span. The molecular form, in which nutrients fulfill their biological functions, determines the biochemical steps necessary to make them phloem mobile. A certain percentage of many nutrients is biochemically inert, and cannot be remobilized (Marschner, 1995; Killingbeck, 2004). Cell wall components are a good example, and explain why fully senesced (dead) leaves are usually rich in carbon as compared to nitrogen. Some macronutrients, including carbon, nitrogen, phosphorus and sulfur, are covalently bound in myriads of both low-molecular-weight metabolites and macromolecules. Proteins and nucleic acids are important stores of nitrogen, phosphorus (nucleic acids) and sulfur (proteins); these macromolecules have to be degraded by specific hydrolases prior to phloem loading and transport. Metals (both macro- and micronutrients) can also be tightly bound, mostly by macromolecules, e.g. cell wall compounds or proteins. Their release is therefore often linked with the degradation of the functional complexes/macromolecules, to which they belong.

5.3 Carbon

Because it is taken up in gaseous form and a large amount of energy is needed for its reduction prior to its incorporation into metabolites, carbon occupies a special position in plant metabolism. Additionally, as discussed obove, degradation of the photosynthetic apparatus is an early event during leaf senescence, leading to a decrease of photoassimilate production and export to sinks, and to an increasing dependence of senescing tissues on respiratory metabolism (Gepstein, 1988; Feller & Fischer, 1994). Metabolization and, to some degree, remobilization of reduced carbon are therefore important for senescing leaves. In this context, Gut and Matile (1988, 1989) observed an induction of key enzymes of the glyoxylate cycle, isocitrate lyase and malate synthase, in senescent barley leaves. Based on these data, and based on low respiratory quotients (0.6), these authors suggested a

reutilization of plastidial (thylakoid) lipids via *β*-oxidation, glyoxylate cycle and gluconeogenesis, allowing export of at least some of the carbon 'stored' in plastidial lipids from the senescing leaf. These observations have since been confirmed and extended (Pistelli *et al.*, 1991; Graham *et al.*, 1992; McLaughlin & Smith, 1994). He and Gan (2002) have shown an essential role for an *Arabidopsis* lipase in leaf senescence; however, it is not yet clear if this or other lipases are involved in preparing substrates (free fatty acids) for *β*-oxidation and gluconeogenesis. Roulin *et al.* (2002) have found an induction of (1→3, 1→4)-*β*-d-glucan hydrolases during dark-induced senescence of barley seedlings, suggesting a remobilization of cell wall glucans under these conditions.

Using radioactive labeling studies,Yang *et al.* (2003) demonstrated considerable remobilization of pre-fixed 14C from vegetative tissues to grains in senescent wheat plants. Interestingly, this process was enhanced under drought conditions, when leaf photosynthetic rates declined faster. Together, these data suggest that while C remobilization during leaf senescence has received less attention than N remobilization, it probably makes important contributions to seed development, at least in annual crops.

5.4 Sulfur

Besides carbon and nitrogen, sulfur is the third nutrient, which (relative to its main form of uptake, sulfate) is reduced by plants prior to its incorporation into certain metabolites and macromolecules. It is noteworthy, however, that plants also contain oxidized ('sulfated') sulfur metabolites (Crawford et al., 2000). Identically to carbon and nitrogen, sulfur is an essential element of both low-molecular weight compounds (including the protein amino acids cysteine and methionine) and macromolecules (proteins). Glutathione (γ -glutamyl-cysteinyl-glycine) represents the quantitatively most important reduced sulfur metabolite; it can reach millimolar concentrations in chloroplasts (Rennenberg and Lamoureux, 1990). Sulfur remobilization from older leaves has been shown; however, the extent of its retranslocation appears to depend on the nitrogen status, at least in some systems (Marschner, 1995). Sunarpi & Anderson (1997) demonstrated the remobilization of both soluble (non protein) and insoluble (protein) sulfur from senescing leaves. This study also indicated that homoglutathione (containing β-alanine instead of glycine) is the principal export form of metabolized protein sulfur from senescing soybean leaves.

5.5 Potassium

Next to nitrogen, potassium is the mineral nutrient required in the largest amount by plants. It is highly mobile within individual cells, within tissues and in long-distance transport via the xylem and phloem (Marschner, 1995). In contrast to the nutrients discussed above, potassium is not metabolized, and it forms only weak complexes, in which it is easily exchangeable. Next to the transport of carbohydrates and nitrogen compounds, potassium transport has been studied most intensely, using both physiological and molecular approaches (Kochian, 2000). Many plant genes encoding K+ transporters have been identified, and some of them have been studied in detail in heterologous systems, such as K+-transport-deficient yeast mutants. Similarly to the situation discussed for nitrogen transport, analysis of K+ transport is complicated by the

fact that these transporters are organized in multigene families with (partially?) redundant functions (Kochian, 2000). Potassium was repeatedly reported to be remobilized in significant quantities from senescing tissues (Hill *et al.*, 1979; Scott *et al.*, 1992; Tyler, 2005). However, it has to be considered that this element easily leaches from tissues, especially senescing tissues (Tukey, 1970; Debrunner & Feller, 1995). Therefore, actually remobilized potassium quantities may be smaller than those reported in the literature.

5.6 Phosphorus

Unlike carbon dioxide, nitrate and sulfate, phosphate (main form of P uptake) is not reduced, but utilized in its oxidized form by plants (Marschner, 1995), both in lowmolecular- weight metabolites and in macromolecules (nucleic acids). Studies on P remobilization from senescing leaves are scarce. Snapp and Lynch (1996) concluded that in maturing common bean plants, leaf P remobilization supplied more than half of the pod plus seed phosphorus. In contrast, Crafts-Brandner (1992) observed no net leaf P remobilization during reproductive growth of soybeans cultivated at three different P regimes. Therefore, while P is a mobile nutrient, its remobilization may be influenced by a number of exogenous and endogenous/genetic factors, making generalizations on the importance of its remobilization difficult. Nucleic acids (especially RNA) constitute a major phosphorus store but, depending on the species and growth condition investigated, considerable P amounts are also present in lipids, in esterified (organic) form, and as inorganic phosphate (Hart & Jessop, 1984; Valenzuela *et al.*, 1996). Similarly to the situation with nitrogen 'bound' in proteins, release of phosphorus from nucleic acids depends on the activities of hydrolytic enzymes. A decrease in nucleic acid levels is typical for senescing tissues, and increases in nuclease activities have also been observed (Feller and Fischer, 1994; Lers *et al.*, 2001), indicating that if P is remobilized from senescing tissues, at least part of it is derived from the degradation of RNA and DNA.

5.7 Magnesium, calcium and micronutrients

Magnesium has not often been considered in studies on nutrient remobilization. However, despite the fact that this element is considered phloem mobile (Marschner, 1995), available results indicate a tendency of continued accumulation during leaf senescence (Killingbeck, 2004). Unsurprisingly, calcium, which is the least mobile of all macronutrients (Marschner, 1995), has repeatedly been found to increase in senescing leaves (Killingbeck, 2004).

Information on remobilization of micronutrients does not allow a generalized picture. For several of them, including Fe, Cu, Mn (which is the least phloem mobile among the micronutrients) and Zn, both remobilization from and accumulation in senescing leaves have been reported (Killingbeck, 2004, and references cited therein). Tyler (2005) gives a broad overview of the fate of numerous elements (including the micronutrients Fe, B, Mn, Zn, Cu, Mo and Ni) during senescence and decomposition of *Fagus sylvatica* leaves; however, in view of the results cited above, it is probably not possible to generalize conclusions from this study, e.g. with regard to the situation in annual crops.

6. Conclusions

This paper discussed some results relating to nutrient remobilization during leaf senescence.Complex regulatory network controlling senescence in plants may be the result of selection pressure driven by different environmental stresses for the development of senescence.Focus on limited number of model plant systems studied by plant senescence scientists may be required for more efficient research, and is likely to be highly relevant to agriculture as well as to our basic understanding of the senescence process in plants.

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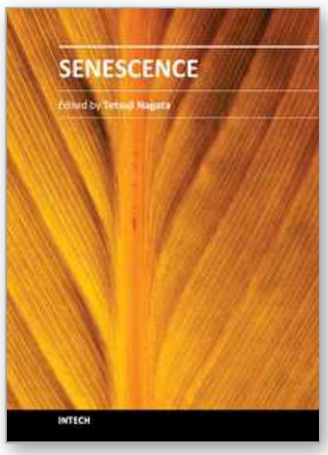

Senescence

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The book "Senescence" is aimed to describe all the phenomena related to aging and senescence of all forms of life on Earth, i.e. plants, animals and the human beings. The book contains 36 carefully reviewed chapters written by different authors, aiming to describe the aging and senescent changes of living creatures, i.e. plants and animals.

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