

## Leaf Senescence as an Important Target for Improving Crop Production

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### Leaf Senescence

Leaf senescence refers to the terminal phase in a leaf's life history. It is a genetically programmed self-attrition program accompanied by recycling of nutrition released during degradation of macromolecules such as proteins [1]. In an agriculture setting, leaf senescence is an important trait that is an ideal target for crop improvement, and recent advances in understanding the regulatory mechanisms underlying leaf senescence have made it possible to devise strategies for manipulating senescence for increasing crop yield and improving quality of horticultural crops such vegetables after harvest [2].

There are three major reasons why leaf senescence is a crucial trait. First, a leaf is an organ where carbohydrates, many nutrients and some novel compounds are synthesized. It is the major source for grain filling in crop such as barley, wheat and rice, which is especially true for flag leaves. The photosynthetic longevity of leaves is thus a major determinant of crop yield and biomass accumulation. For example, premature senescence of photosynthetic leaves in soybean induced by abiotic stresses caused a loss of productivity due to a decrease in assimilatory capacity [3]. Another example is hybrid maize; analyses of over 50 years (1930–1980) of hybrid maize data in the USA and nearly 30 years (1959–1988) of maize hybrid yields in Ontario, Canada, found that the late onset of leaf senescence contributed to significant increases in maize yields [4,5].

Secondly, during leaf senescence, not only the green pigment chlorophyll but more importantly many nutrients such as vitamin C and proteins are quickly degraded. Leaf senescence thus reduces the postharvest longevity of foliar vegetables and potted plants, and devalues animal feed.

Thirdly, a senescing leaf becomes more vulnerable to infection by pathogens, especially postharvest fungal pathogens, and some of the fungal pathogens may produce toxic chemicals, rendering our food and animal feed unsafe.

Because of its significance, leaf senescence has been intensively investigated and remarkable advances have been made in the model plant *Arabidopsis thaliana* [6]. It is known that the senescence processes can be regulated by various plant growth substances [7]. It is also known that leaf senescence can be regulated at the transcriptional and post-transcriptional levels (see articles in Plant Molecular Biology special issue on plant senescence, Vol. 82, Issue No. 6, August 2013; see also an upcoming leaf senescence special issue of Journal of Experimental Botany, 2014). Some of the basic findings from *Arabidopsis* have been translated into practical application for manipulating leaf senescence in various agronomic and horticultural crops. Among the strategies are (1) plant hormone (especially cytokinin) biology-based technology, (2) senescence-specific

transcription factor biology-based technology, and (3) translation initiation factor biology-based technology [2].

Cytokinins are a class of plant hormone that inhibits leaf senescence [7]. Isopentenyl transferase (IPT) catalyzes the first and rate-limiting step in the cytokinin biosynthesis in plants. When the promoter of a senescence-specific gene called SAG12 was used to direct the IPT expression, it forms an autoregulatory senescence-inhibition system [8]. Transgenic plants harboring this system displayed significant delay in leaf senescence, substantial increase in yield and biomass, enhanced tolerance to drought and other stresses, and remarked improvement in postharvest performance. Other similar senescence-associated gene promoters have also been used. This cytokinin biology-based technology is approaching commercialization [2].

The transcription factor biology-based technology can be exemplified using AtNAP. AtNAP is a senescence-specific transcription factor that regulates leaf (and fruit) senescence [9,10]. Knocking out or down of this gene in *Arabidopsis* led to nearly 50% increase in leaf's photosynthetic longevity. In principle, knocking out or down of its counterpart gene in a crop should lead to the similarly delayed leaf senescence phenotype and enhanced grain yield. This was well observed in maize and rice. Maize plants with suppressed ZmNAP expression had 15-30% increases in 1000-seed weight, and rice plants with suppressed OsNAP expression showed up to 24% increase in rice grain yield (reviewed in [2]). Most recently, an up to 10.3% increase in rice grain yield was also observed in the OsNAP-down-regulated rice lines [11]. To my knowledge, this technology has been successfully applied to several other crops including soybean and cotton plants.

The translation initiation factor eIF-5A biology-based technology has also been explored in several horticultural crops such as carnation, tomato and banana with improved postharvest performance [2].

In summary, leaf senescence is an imperative trait that negatively impacts on crop yield and quality. With the increasingly understanding of regulatory mechanisms of leaf senescence, emerging new technologies targeting the leaf senescence trait have been, and will continue to be, developed for crop improvement.

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