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This Week's Citation Classic®

Martin C & Thimann K V. The role of protein synthesis in the senescence of leaves. I. The formation of protease. *Plant Physiol.* 49:64-71, 1972.
[Crown College, University of California, Santa Cruz, CA]

The progress of senescence was characterised by protein synthesis, chlorophyll loss, marked increases in protease activity, and proteolysis. The synthesis of proteases appeared to be of prime importance since substances that suppressed senescence (cycloheximide and kinetin) also inhibited the development of protease activity. [The *SCI*® indicates that this paper has been cited in over 210 publications.]

C.C. Martin
Southedge Research Station
Queensland Department of Primary Industries
P.O. Box 174
Mareeba, Queensland 4880
Australia

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The research for this *Classic* article was carried out in the Thimann Laboratories, University of California, Santa Cruz, when K.V. Thimann was provost of Crown College. The system used to investigate senescence was comprised of apical segments of primary oat leaves left to senesce in the dark.

At the start of our research, generally accepted views of senescence were that the marked proteolysis, which characterised senescence, was due to decreased protein synthesis combined with a steady rate of breakdown[1] and that hormones delayed senescence by maintaining protein synthesis directed by DNA-dependent RNA synthesis.[2] The evidence presented to support this viewpoint was rather complicated and tenuous, since my predecessor at Santa Cruz had shown the opposite: that kinetin delayed senescence by preventing proteolysis, not by affecting protein synthesis.[3] This, I feel, partly explains why our paper was cited frequently. In contrast to the prevailing views of senescence, our concept was simple, direct, and tangible; the marked proteolysis was due to an increase in proteases. It is very difficult to explain increased proteolysis *via* decreasing protein synthesis when the rate of bulk leaf protein synthesis in mature leaves is low. In addition, the evidence we presented was convincing; the progress of senescence was accompanied by increased protease activity, and both cycloheximide and kinetin suppressed the increase and were very effective in delaying senescence.

Until August 1970, when some aspects of senescence were presented in a paper to the American Society of Plant Physiologists at a meeting in Bloomington, Indiana, I believed we had a plausible case. In conversation with Joe Varner, then president of the American Society of Plant Physiologists and now at Washington University, St. Louis, Missouri, one evening after the meeting, I was left in no doubt that Varner felt I was on the wrong track. The problem was protein synthesis. On the one hand, we presented evidence that cycloheximide, by inhibiting protein synthesis, delayed senescence. On the other hand, the "prevailing view" was that kinetin suppressed senescence by maintaining protein synthesis. It is now recognized that cycloheximide almost universally delays senescence.[4]

The reaction to our first attempt to publish some results was much more severe than Varner's criticism. One reviewer included what I interpreted as a personal attack on Thimann. I could understand reviewers rubbishing the work but not the people involved. On discussing this with Thimann, he said, "Don't worry. They think it happens differently. We need more evidence on protease activity. The work so far is good. That graph depicting the progression of senescence is the type that finds its way into textbooks."

In retrospect, the most satisfying aspects about the work were: first, my participation in the development of a system and techniques that are still being used to produce results,[5] and second, that we were essentially correct about the involvement of proteases. They have since been purified and characterised.[6]

1. **Woolhouse H W.** The nature of senescence in plants. *Symp. Soc. Exp. Biol.* 21:179-213, 1967. (Cited 120 times.)
2. **Osborne D J.** Interactions of hormonal substances in growth and development of plants. *J. Sci. Food Agr.* 16:1-13, 1965. (Cited 70 times.)
3. **Shibaoka H & Thimann K V.** Antagonisms between kinetin and amino acids. *Plant Physiol.* 46:212-20, 1970. (Cited 70 times.)
4. **Thomas H & Stoddart J L.** Leaf senescence. *Annu. Rev. Plant Physiol.* 31:83-111, 1980. (Cited 130 times.)
5. **Veierskov B, Satler S O & Thimann K V.** Metabolism of oat leaves during senescence. VIII. The role of L-serine in modifying senescence. *Plant Physiol.* 78:315-9, 1985.
6. **Drivdahl R H & Thimann K V.** Proteases of senescing oat leaves. I. Purification and general properties. *Plant Physiol.* 59:1059-63, 1977. (Cited 40 times.)

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