Postharvest Senescence: An Introduction to the Symposium

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First we ripen, then we rot Hayflick (7)

Senescence has long been a concern of postharvest scientists. The essential interests are two-fold. On the one hand, the premature senescence of many commodities, often accelerated due to adverse handling and storage conditions, renders them useless to the consumer. On the other hand, for many other commodities, notably fruits and cut flowers, the early manifestations of senescence form the basis of desirable quality attributes. The objectives of postharvest handling practices in the latter case are to: a) arrest continued development during storage and b) ensure that normal development occurs following storage. For these reasons, an appreciation of the underlying causes of senescence becomes crucial to our understanding of how best to control and regulate the process. The symposium speakers will focus on the mechanisms and control of senescence in three horticultural commodity groups: leafy vegetables, fruits, and cut flowers.

Although plant researchers have long had an interest in senescence and in particular plant longevity (see ref. 15 for an early treatise), numerous early textbooks failed categorically to mention the subject. One that did (13) stated only that "dying of plants may be regarded as a phenomena analogous to senescence of an animal organism." Wright (27) commented on the "unexpected state of affairs" in noting that senescing apples were capable of net protein synthesis (9). These writings and others emphasized the then-prevailing thinking that senescence reflected dying and was perhaps worthy of little further consideration. After 1940, research interest in plant senescence increased markedly, as did emphasis on the relevance of senescence to postharvest horticulture (e.g., refs. 1, 19, 23, 24). Several recently published books contain a number of chapters devoted to various features of postharvest senescence in each of the three commodity groups (11, 21).

Throughout the early period of plant senescence research, the term senescence remained somewhat ill-defined and often was employed interchangeably with aging. Leopold (10) defined senescence as "the deteriorative processes which naturally terminate the functional life of an organ, organism, or other life unit." Other definitions were largely derived from this, at least in concept if not in prose. Watada et al. (25) recently published definitions of developmental terms, applicable on a cross-commodity basis, for use by postharvest scientists. Senescence was defined as "those processes that follow physiological maturity or horticultural maturity and lead to death of tissue." Aging, in contrast, is interpreted in a broader context as changes occurring with the passage of time, as originally proposed by Medawar (14). Although plant scientists have developed a rather clear distinction in the meanings and usage of the terms senescence and aging, the two continue to be employed quite interchangeably in the literature dealing with the demise of organisms other than plants. This apparently causes few problems, except for plant scientists who may elect to read the papers.

Leopold (10) has defined four major morphological patterns of senescence in higher plants. These patterns include overall senescence, top senescence, deciduous or organ senescence, and progressive senescence. He further suggested a basic mechanistic equivalence in the types, perhaps differing only in the intensity of the physiological signal and reflecting the adaptative functions of senescence. From a postharvest standpoint, our interests generally are directed at senescence in individual organs or organ systems. The senescence of cut flowers, typically assessed on the basis of corolla development, represents an interesting interplay of different organs (gynoecial vs. petals) and equally interesting are marked differences, e.g., in ethylene biosynthesis, between morphological regions within individual petals (16). Undoubtedly, physiological differences exist in the organs and tissues of many commodities harvested as multi-organ structures.

The expression of senescence in plants is a characteristic feature of all hierarchies of structural organization, from whole organism down to the molecular. Studies of the latter have provided conclusive evidence for the role of the genome in certain types of plant senescence, most notably in fruit (5). Although these studies dealt primarily with the role of gene expression in ripening vs. senescence per se, it is difficult to draw a clear physiological or temporal distinction between the two developmental stages (19). The differences between senescence of leaves and flowers on the one hand and fruit on the other may reside in the temporal relationship between senescence and execution of organ function. The seed dispersal role of fruits is dependent, to various degrees, on the timely expression of physiological and other attributes that collectively constitute senescence. Thus, ripening may be viewed appropriately as a functionally modified, protracted form of senescence. The lack of evidence for new gene expression in senescing vegetative tissues does not preclude the involvement of programming. Evidence for a potential role of long-lived mRNA and the orderly sequence of cellular events attest to the tight regulation and control of leaf senescence (22). A comparison of the characteristic features of leaf and fruit senescence was the subject of a recent book chapter (4).

A factor of significant importance in a consideration of the senescence of harvested commodities is that of stress. The problem can be particularly acute for commodities that are typically harvested immature, at a time prior to the cessation of physical growth. Organs so harvested do not maintain metabolic homeostasis and are particularly subject to rapid senescence. The capacity of these and, in fact, most commodities, to survive following harvest depends, in part, on what Pearl (17) has termed inherent vitality, "the capacity of an organism to perform vital actions in the absence of exogenous...matter or energy." Flowers represent a notable exception to this situation in that the provision of an exogenous carbon source will ensure continued development of those types harvested immature and delay senescence in all cut flowers. Aside from the obvious trauma of harvest, stress may be imposed via subsequent disturbance in water balance or through mechanical, chemical, or pathogenic injury. All of these factors may serve, either directly or indirectly, to accelerate senescence and shorten postharvest longevity. However, as postharvest scientists well appreciate, the strong influence of environmental and other external factors on senescence has also resulted in the implementation of storage conditions designed to effectively decelerate the process. Low-temperature, atmospheric modification (CA, hypobaric), and exogenous ethylene removal are some major examples.

The practical benefits to be derived from understanding the cellular basis of senescence have led to the formulation of a number of theories to explain it. Understandably, the theories generally have been expressed on the basis of assessments of cellular changes observed during the early course of the senescence syndrome. The problem is, then, one of separating cause and effect. Sacher (18) has lamented the growing number of what he has termed "aspect theories"—those emphasizing the importance of isolated symptomatic events while ignoring the possibility of a more fundamental cause. The occurrence of qualitatively unique gene expression would certainly appear to qualify as the fundamental cause of fruit senescence, for example; however, it is clear that, during the period following the cessation of physical growth [Pearl's (17) "period of suspended animation"] the organ does not reside in a metabolically static state. Consider as but one example the ever-changing status

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of ethylene sensitivity. Strehler (20), in considering the postulated mechanisms of aging in mammals, classified all senescence-related processes into two categories. The determinate changes are those representing an intrinsic portion of the developmental scheme. The ancillarly or stochastic processes, on the other hand, emphasize the role of deleterious environmental events. The two are clearly not mutually exclusive. Although developmentally controlled cell death is a common occurrence during the ontogeny of most organisms, Sacher (18) has argued that there are serious flaws in logic (and no evidence) in arguing that aging in mammals is actively (i.e., developmentally) programmed. Hayflick's (8) classic studies demonstrating the finite replicate capacity of cultured human fibroblasts clearly emphasized the role of the nucleus in cellular aging, but he does not consider this to represent a programmed phenomenon in a strict sense. Rather, the suggestion has been made that aging occurs as a result of information (programming) depletion (6, 7), and that longevity is a consequence of the constitution or status of "longevity assurance genes" (2, 19). The action of these genes would be to forestall or amend the cumulative effects of stochastic processes (e.g., somatic mutations, dysfunctions in information processing, free radical damage) influencing the capacity of an organism to maintain homeostasis.

The convincing evidence that in plant organs senescence is developmentally regulated, and thus determinate in nature, offers unique possibilities for controlling it but in no way answers the question of how it is mediated. An obvious question might then be asked as to what factors (activators/repressors) have changed to permit altered gene expression (12). Furthermore, the determinate nature of senescence in no way dictates that all forms of organ senescence are mechanistically identical. In an early review, Crocker (3) emphasized that is was impossible to discuss the aging of plants under a single concept. More recently, Woolhouse (26) commented, referring to natural plant senescence, that "there are many different ways of getting dead."

There are indeed many ways of getting dead. The refinement of handling and storage techniques coupled with biological and genetic manipulation will serve collectively to render senescence more precisely regulated and result in greater availability and quality of harvested horticultural commodities. In the final analysis, we might ask ourselves what we foresee as our final goal in the quest for ever-increasing postharvest longevity. At what point do these aspirations conflict with the well-being of our growers and producers? As Frederick the Great is said to have quipped to his troops (2), "Sons of bitches, do you want to live forever?"

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Senescence of Leafy Vegetables

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Before undertaking this survey of senescence in stored leafy vegetables, I thought that there would be a wealth of information available from which I could draw. I was in for a surprise. Even though there exists ample literature on some symptoms of senescence among leafy vegetables, amazingly little research has been published regarding fundamental changes in their physiology as senescence progresses. Among the roughly 100 papers I checked for this presentation, only a few dealt with any basic aspect of hormonal influences on senescence in leafy vegetables (2, 15, 40, 47, 57). I was amazed by this relative neglect of studies of senescence in a group of crops that are of major economic importance. If this symposium does little more than point to where the gaps in knowledge are, it can be considered a success.

Most basic research on senescence has involved studies of seedlings or leaves that are not used as food by human beings. Nevertheless, we must consider results obtained with leaves of oats, rice,