

## Regulation of assimilation and senescence by the fruit in monocarpic plants

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For most monocarpic species studied, blocking fruit development prevents or at least delays the death of the plants. However, it usually does not prevent the decline in photosynthetic rate, while it may or may not maintain the photosynthetic components (machinery) such as chlorophyll and ribulose 1,5-bisphosphate carboxylase. Since sink demand influences photosynthetic rate and the fruit-less plants have limited sink capacity, their reduced photosynthesis may represent a metabolic adjustment but not senescence. The exact causes of the variable decreases in photosynthetic components in fruit-less plants are uncertain. The causes of metabolic decline may be different in reproductive-phase monocarpic plants with and without fruit. In any case, assimilation rate, i.e. photosynthesis, may not always provide a reliable index of senescence. Whether or not the developing fruits of monocarpic plants actually control the early and intermediate decline of metabolism is not clear; however, at least in soybean under non-stress conditions, they cause the final decrease and death.

*Key words* – Dry weight accumulation, fruit removal, *Glycine max*, monocarpic senescence, nitrogen fixation, photosynthesis, sink demand, soybean.

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### Introduction

Senescence is an internally regulated degeneration leading to death of cells, organs or whole organisms (Leopold 1961, Noodén 1988a). As the fruits develop on monocarpic plants (a single reproductive phase), the plants degenerate (monocarpic senescence) and die. The correlation between the fruit development and monocarpic senescence, plus the fact that removal of the reproductive structures can prevent this quick death in many monocarpic species, e.g. soybean, has given rise to the idea that the reproductive structures cause the death of monocarpic plants (Molisch 1938, Noodén 1980a, 1988b). Likewise, decreased metabolism is widely accepted as an index of senescence (Noodén 1988a). Recently, numerous observations (Tab. 1) of metabolic decline in fruit-less reproductive-phase plants, especially in leaves of depodded soybeans, have called for reexamination of these ideas. In addition,

similar metabolic declines occur during the reproductive phase of male-sterile and male only monocarpic plants (Weiling 1941, Leopold et al. 1959; Tab. 1), which do not produce fruits.

Here, we try to unify and reconcile some of these diverse and fragmentary observations on the regulation of senescence and assimilation. This should also eventually yield a better understanding of how the whole plant regulates and integrates its activities. Because of the centrality of leaf degeneration to monocarpic senescence, at least in soybean (Noodén 1980b, 1988b), that organ will be emphasized here; however, changes in other structures, particularly the roots, will be noted. Since the data are most extensive for soybean, that species will be emphasized. Even though the soybean serves to illustrate the general principles, which may be extended to other species, it must be noted that there are some variations in the controls of monocarpic senescence among different species (Noodén 1980a).

*Abbreviations* – ABA, abscisic acid; Chl, chlorophyll; NCER, net carbon exchange rate; RuBPcase, ribulose-1,5-bisphosphate carboxylase.

### Sink control of assimilation

Evidence that C assimilation (photosynthesis) adjusts to sink 'demand' comes from a great number and variety of experimental manipulations of source-to-sink ratios (King et al. 1967, Neales and Incoll 1968, Geiger 1979, Herold 1980). They have been carried out not just on reproductive plants but also on vegetative plants, and they include partial or complete removal of competing sinks and shading or partial removal of the source leaves. For example, increasing the sink-to-source ratio by partial defoliation or partial shading stimulates photosynthesis in the remaining or unshaded leaves of wheat (King et al. 1967) and soybean (Thorne and Koller 1974, Peet and Kramer 1980). Parallel cases of sink promotion of photosynthesis also occur during normal development. Photosynthesis in wheat, soybean, pepper, apple and many other plants often increases early in fruit growth, when the fruits' consumption of carbohydrates and nitrogen is rising rapidly (Dornhoff and Shibles 1970, Rawson et al. 1976, Lenz 1977, Hall and Milthorpe 1978, Watson and Casper 1984, Shibles et al. 1987). Similarly, pod loads greater than normal seem to enhance photosynthesis in soybean (Seddigh and Jolliff 1984, Lauer and Shibles 1987). Likewise, increased N<sub>2</sub> fixation with its high energy demand also seems to promote photosynthesis (Imsande 1988). Conversely, defruiting dramatically decreases photosynthesis in the supplier leaves of pepper (Hall and Brady 1977, Hall and Milthorpe 1978), wheat (King et al. 1967) and barley (Nösberger and Thorne 1965). Sink consumption may also influence other assimilatory processes in addition to photosynthesis. For example, blocking pod development may reduce the accumulation of some minerals, e.g. K and P (Kollman et al. 1974, Derman et al. 1978, Noodén and Mauk 1987) and N<sub>2</sub> fixation (Peat et al. 1981, Schweitzer and Harper 1985). However, the effects differ depending on the element and environmental conditions, and in some cases, N accumulation is not changed (Crafts-Brandner et al. 1984c, Israel et al. 1985). Sometimes, though, source-sink alterations do not affect photosynthesis in the source (Geiger 1979); these could be special situations. For example, where photosynthesis is already at its capacity, neither increased sink load nor partial defoliation would increase the photosynthetic rate in the remaining leaves. Nonetheless, sink 'demand' usually can influence the assimilatory metabolism of the supplier organs.

It is now widely recognized that source-sink interactions are complex, because the plant may adjust itself as normal development proceeds or in response to experimental manipulations. In particular, removal of the reproductive structures not only eliminates sinks and may

delay senescence (to be discussed below) but may allow alternative sinks to replace those removed. For example, excision of wheat heads promotes the growth of vegetative tillers. Thus, deheading decreases photosynthesis in the major supplier leaf (flag leaf) only if the growing parts of the vegetative tillers are removed (Rawson et al. 1976). In the one case (*Phaseolus vulgaris*; Tamas et al. 1981) where fruit removal actually stimulates photosynthesis, it also promotes growth of axillary buds and probably other vegetative parts. Earlier recognition of the differences among species and the variety of possible responses to source-sink alterations could have avoided much unnecessary disagreement. Hopefully, this lesson can be applied to the subject of this review along with the need for patience in integrating diverse data in whole-plant studies.

On the other side of the source-sink interaction, sources may also actively send assimilates to the sinks (Noodén 1980a, 1988a). For example, leaves may continue to move photosynthate and other assimilates basipetally even after their detachment from the rest of the plant and thereby the primary sinks (Leonard 1939, Thimann et al. 1974).

How do sinks regulate their suppliers or exert their 'demand' on photosynthesis and other assimilatory processes? Active sinks such as developing fruits do not function only in a passive way by consuming soluble nutrients and thereby driving a mass flow system. For example, unloading from the phloem in seed coats connected to the plant continues to supply nutrients to the empty seed coat cup for 24 h after the embryos have been removed (Thorne 1985, Ho 1988). Moreover, flower buds, flowers and young fruits seem to stimulate N<sub>2</sub> fixation (Peat et al. 1981) in spite of the small amounts of N they accumulate. Possibly, sinks send hormonal regulatory signals to the supplying organs to regulate their activity (Noodén 1984, 1988a). The well-studied cases of embryos signalling mobilization of stored nutrients in germinating seeds support this idea (Noodén 1988a).

Adjustment of photosynthesis to sink demand might be achieved through changes in stomatal or mesophyll conductance over the short and long term, respectively, and this may be mediated by ABA. Normally, ABA produced in the leaves flows to the fruits. Thus, fruit removal causes ABA levels to rise, stomata to close (Lenz and Williams 1973, Kriedemann et al. 1976, Goldbach et al. 1977, Koller and Thorne 1978, Setter et al. 1980) and the photosynthetic machinery to decrease in the leaf blades (Raschke and Heidrich 1985).

### Changing sink 'demand' in monocarpic plants

One of the most striking features of monocarpic plants is the sharp shift in resource investment from the vegetative to the reproductive parts (Noodén 1980a, 1988b). Root growth, stem growth (elongation and thickening), and leaf production decrease and usually cease early in

the reproductive phase due at least in part to cessation of meristematic activity. With the vegetative sinks (growth) mostly gone, the reproductive structures provide the main sinks, but eventually, these also cease.

In some monocarpic species such as *Reseda odorata* (Molisch 1938), removal of the reproductive structures can restore vegetative growth; however, in others such as wheat, corn and soybean, this procedure has little effect. Nonetheless, root and stem growth (thickening) may be promoted somewhat, albeit variably, by this means in soybean (Noodén 1980a, 1984, 1988b, Alberda and Witlage-de Boer 1983). Likewise, additional starch and K may accumulate in the leaves and stem of the depodded soybean plants (Kollman et al. 1974, Derman et al. 1978, Mondal et al. 1978). Thus, vegetative sinks may replace the reproductive sinks when development of the latter is blocked, but usually this replacement is limited.

### **Dry weight accumulation in monocarpic plants lacking fruits**

Recently, much emphasis has been placed on the continued dry weight accumulation in fruit-less, reproductive-phase monocarpic plants, especially soybean (Tab. 1). These data imply that the overall assimilation rate for fruit-bearing plants may not differ greatly from comparable fruit-less plants and thereby suggest that the fruits may not regulate the metabolic decline in monocarpic plants; however, there are some complications. Simple dry weight measurements, even if they are complete with data for roots and fallen leaves, do not present the whole picture of the energy consumption, for the metabolic cost of the abundant fats in soybean seeds is much greater than the predominantly carbohydrate material that constitutes most of the dry matter in other parts of the plant (Penning De Vries 1975), and therefore the assimilatory metabolism of pod-less plants may be somewhat less than that of podded plants even if the dry weights are similar. Paradoxically, photosynthesis may decline without a parallel change in dry weight accumulation (Wittenbach 1982, 1983). Perhaps these measurements of photosynthesis are incomplete, because they are taken for only one leaf and at one point during the day rather than integrating activity over a 24-h period. Regardless of these details, sink activity represented by dry weight accumulation generally appears to decrease in fruit-less plants, but is this due to sink or source (assimilatory) limitation? Inasmuch as growth seems to be restricted in the fruit-less, reproductive-phase plants, it appears that these plants are sink limited. Perhaps more important, while dry weight accumulation declines in comparable fruit-less and fruit-bearing plants, the key difference is that the final metabolic decline and death are delayed by blocking fruit development in many monocarpic species, e.g. soybean.

### **Metabolic decline in fruit-less plants**

Assimilatory processes and metabolism in general decrease in monocarpic plants, at least during late reproductive development, and this is a prelude to death (Noodén 1980a, 1988a, b). Given the importance of metabolic decline in senescence and the fact that defruiting prevents (or at least greatly delays) death in soybean and many other monocarpic plants, it is interesting that the photosynthetic components, e.g. Chl and RuBPcase, may not decrease even where photosynthesis drops in fruit-less soybean (Tab. 1) and other plants (Noodén 1980a, 1988b). In corn and wheat, ear removal may delay or promote the loss of leaf Chl, RuBPcase and various activities, but the exact response depends on the variety and probably also on environmental conditions (Allison and Weinmann 1970, Feller 1979, Patterson and Brun 1980, Crafts-Brandner et al. 1984a, Crafts-Brandner and Poneleit 1987).

It may, however, be difficult to get accurate measurements of Chl, RuBPcase, etc in older leaves (Noodén 1988a). In soybean especially, but also in some other species, the leaves contain very high levels of phenolics, and these increase 4- to 5-fold in both podded and pod-less plants (Burke et al. 1984). These and the quinones derived from them could be expected to bind to proteins, thereby interfering with both enzymic and immunological assays (Singleton and Kratzer 1973, Loomis 1977, Grover and Sinha 1985). Thus, reports that RuBPcase or any other enzyme disappears entirely in the living, green leaves of pod-less soybeans may be underestimates. A parallel problem may hold for Chl determinations where degradation during extraction may lower the values (Noodén 1988a). Nonetheless, it seems likely that the photosynthetic machinery often does decline, but this occurs on a variable basis.

### **Main aspects of the metabolic decline**

Three aspects of this mass of observations on the metabolic decline in fruit-less plants warrant special consideration: A) Why is there such variability in the decline of the photosynthetic machinery? B) Does the metabolic decline of fruit-less plants represent senescence or an adjustment to sink loss? C) Does the decline in defruited plants necessarily go to completion, i.e., death?

A) Why do metabolic components such as Chl and RuBPcase sometimes decrease and other times not (Tab. 1) in fruit-less soybean plants, where photosynthesis decreases? Genetic factors are clearly important (Crafts-Brandner and Egli 1987a); however, these variations are not just varietal differences. For example, in one particular variety of soybean, Williams, Chl and RuBPcase levels remain high in the pod-less plants under one set of conditions (Schweitzer and Harper 1985) but decrease greatly under another (Wittenbach 1983). A more direct comparison can be made in sunflower plants (Ho et al. 1987) where deheading prevents Chl

Tab. 1. Soybean responses to sink reduction. Dry matter accumulation, photosynthesis and photosynthetic capacity. nd, No data.

Treatment	Culture conditions	Sink reduction effects on:		Photosynthetic components		Other observations	Reference
		Dry matter accumulation	Photosynthesis (most are single leaf measurements)	Chlorophyll	RuBPcase		
Partial depodding	glasshouse, hydroponics	- no overall change	- nd	- nd	- nd	- root growth enhanced - fallen leaves not included	Lenz and Williams, 1973
	field	- nd	- decreased (NCER of the whole canopy) in early pod development - plateauing not known	- nd	- nd	- nd	Lawn and Brun, 1974
	glasshouse, hydroponics	- possibly increased	- nd	- nd	- nd	- root and stem growth promoted more than usual - fallen leaves not included - unusually large plants (250 g dry weight)	Loong and Lenz, 1974
	glasshouse	- nd	- delayed decline (NCER) slightly - plateaued at about 15%	- nd	- nd	- nd	Woodward and Rawson, 1976
	field	- nd	- no effect (NCER) - plateauing not known	- nd	- nd	- nd	Lauer and Shibles, 1987
Male sterility (10-15% podset and pod dry weight relative to normal plants)	glasshouse, hydroponics	- nd	- enhanced decline	- nd	- nd	- nd	Huber et al. 1983
	glasshouse, hydroponics	- nd	- nd	- loss plateaued at 60%	- nd	- the basic thylakoid network was retained	Burke et al., 1984
	field	- nd	- nd	- plateaued at 95%	- loss delayed - plateaued at 50-90%	- in one year, Chl dropped due to drought after plateauing	Schweitzer and Harper, 1985
	glasshouse, hydroponics	- nd	- nd	- nd	- nd	- decreased PSII electron transport in male-sterile plants - no changes in PSI electron transport	Burke et al., 1987

loss in glasshouse-grown but not in field-grown plants. Many of the plants grown in the field faced adversities, including limiting rainfall plus unfavorable temperatures; and probably they accumulated disease at the end of the growing season and even a water deficit under clear, sunny skies. Quite mild water stress may be sufficient to promote Chl loss, for we (A. Velasco, B. J.

Murray and L. D. Noodén, unpublished data) find that low humidity accelerates leaf yellowing in soybean explants (a stem cutting with a leaf and one or more pods) even though the explant base is immersed in water. Stress does influence senescence, but this interaction is not well understood (Noodén 1988a). In any event, environmental stress, particularly mild water stress,

Tab. 1. Continued.

Treatment	Culture conditions	Sink reduction effects on:		Photosynthetic components		Other observations	Reference
		Dry matter accumulation	Photosynthesis (most are single leaf measurements)	Chlorophyll	RuBPcase		
Complete (continuous) depodding	environmental control chambers, hydroponics	– decreased 11%	– nd	– nd	– nd	– roots and fallen leaves included	Derman, Rupp and Noodén, unpublished data, 1975
	field	– nd	– increased decline (NCER) – plateaued at about 10%	– loss prevented	– loss prevented	– desinking either 32 h before the measurements or continuously from midbloom produced the same decrease in photosynthesis	Mondal et al., 1978
	environmental control chambers	– nd	– increased decline ( $^{14}\text{CO}_2$ uptake) – plateauing not known	– loss prevented	– loss earlier and accelerated	– the exact effect depends on when the depodding is started	Wittenbach, 1982
	environmental control room, hydroponics	– increased 55%	– nd	– nd	– nd	– fallen leaves included – roots, stems and leaves increased	Alberda and Witlage-de Boer, 1983
	field	– decreased 20%	– increased decline ( $^{14}\text{CO}_2$ uptake) – apparently dropped to zero	– loss delayed slightly, especially near the end – end point not determined	– appears to drop to zero – loss slightly hastened	– refers to node 12 – roots and fallen leaves(?) not included – This is the only case when depodding has almost no effect on Chl loss.	Wittenbach, 1983
	field	– unchanged overall	– nd	– loss delayed – plateaued at 20–30%	– plateaued at 40% or at least delayed	– roots and fallen leaves not included	Crafts-Brandner et al., 1984a, b
	glasshouse	– rate unchanged but duration longer	– no apparent decline (NCER) in deflowered plants, at least up to late podfill in controls	– nd	– nd	– roots and fallen leaves included	Heitholt and Egli, 1985
	field	– nd	– delayed decline in two cultivars – plateaued at 10–20% in one of the delayed varieties	– loss delayed – end point not determined	– loss delayed in two cultivars but slightly accelerated in one	– nd	Crafts-Brandner and Egli, 1987a

may be an important modulator of the loss of the metabolic machinery in fruit-less plants.

B) Does the metabolic decline in fruit-less plants necessarily represent senescence in the sense that it is

part of the sequence leading to death? First, it needs to be recognized that not all downward adjustments of metabolism are associated with senescence (Noodén 1988a). Second, as explained above, the decreased sink

capacity in fruit-less plants seems to be an important factor in the reduction in photosynthetic rate. Thus, a distinction should be made between the decreases in photosynthetic rate and the decreases in photosynthetic components such as Chl and RuBPCase. The rate may decrease without a concomitant decrease in the components or capacity. The former certainly could be a sink effect, while the latter may be more representative of monocarpic senescence (Noodén 1988a, b). The diminution of the photosynthetic components in fruit-less plants seems to depend on environmental factors; that is, stress may be a senescence-driving force replacing the fruit effects. It may also be that some loss of activity proceeds independently of the fruit, i.e. the metabolic machinery of leaves may be built to last only so long. Furthermore, reproductive plants may be less able to replace inactivated metabolic components, just as they are less able to regenerate vegetative parts (Noodén 1988b).

C) While defruited plants clearly undergo a metabolic decline, does this necessarily result in death? Where measurements have been continued long enough, photosynthesis in pod-less plants usually declines to 10–25% of the original and then levels off (Tab. 1). Thus, the depodded plants seem to decrease to a new steady-state assimilatory rate, which may reflect their basal metabolic rate, i.e., self maintenance without growth. Whether or not the metabolic decline goes directly to completion probably depends on environmental conditions. Adverse conditions will of course drive this decline to completion, but these plants do not have to die immediately and do not if conditions are favorable. We find that the depodded soybean plants stay green and fresh indefinitely in environmental control chambers or until frost in the field if they are irrigated as needed (Derman et al. 1978, Noodén 1988b). In addition, the cells in the leaves of depodded soybean plants maintain their plasma membrane integrity (dye exclusion) (Artis et al. 1985), which indicates they are still alive (Noodén 1988a).

### Is monocarpic leaf senescence controlled by the pods in soybean?

A wide variety of experimental manipulations show a linkage between pod development and leaf senescence (Noodén 1980a-1988b). Many different kinds of treatments exert parallel effects on pod development and leaf senescence. For example, physical restriction of late pod expansion in soybean delays leaf senescence to the same extent that it delays the late, inductive phase of pod development (Crafts-Brandner and Egli 1987b). In soybeans, the pod (seeds) seem to control at least the late, final phase of metabolic decline, which seems particularly important (Noodén 1980b). It is, however, possible to prevent the death of the leaves on podded plants by treating with antisenesescence hormones or by surgically modifying these plants to separate the pods and

leaves spatially (Noodén 1980a-1988b). In general, the developing fruits seem to induce the death of monocarpic plants; however, there are exceptions, e.g. male only plants (Leopold et al. 1959, Leopold 1961, Noodén 1980a, 1988b) where the mechanism may be different.

### On the nature of senescence

Clearly, some metabolic declines do not represent senescence; this is demonstrated in the sink effects on assimilation discussed above and in other cases (Noodén 1988a). While a decrease in photosynthetic rate is a normal part of the senescence syndrome in monocarpic plants (Noodén 1988a, b), it may not accurately reflect senescence, for it may also be influenced by diminished sink demand. The decline in photosynthesis, which results from a loss of photosynthetic components (e.g. Chl and RuBPCase), rather than effects of sink loss may better reflect monocarpic senescence (Noodén 1988b). Exactly when senescence begins and what constitutes senescence is uncertain (Noodén and Leopold 1978, Noodén 1988a, b); however, recognizing these problems is a prerequisite to resolving them.

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