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Transmission of the Monocarpic Senescence Signal via the Xylem in Soybean[1]

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ABSTRACT

During monocarpic senescence in soybean (*Glycine max* [L.] Merrill cv. Anoka) there is a remobilization of nitrogen from the leaves to the seeds, and it has been hypothesized that this loss of nitrogen from the leaves induces foliar yellowing. The phloem in a small segment of the petiole between the pods and the target leaf can be inactivated with a jet of steam. When a plant is depodded except for a single pod cluster in the center of the plant, the pod cluster induces yellowing of the nearest leaf even if the petiole contains a zone of dead phloem, whereas most of the rest of the plant remains green. The nitrogen content of these leaves with a dead phloem zone in their petioles does not decrease greatly, even though the leaves turn yellow. A similar treatment of a single leaf on a fully depodded plant (leaves stay green) does not cause that leaf to turn yellow. Since nutrients would have to be withdrawn from the leaves via the phloem, the pods do not induce yellowing by pulling nutrients out of the leaf and must be able to exert their influence via the xylem.

Historically, monocarpic senescence has been attributed to nutrient exhaustion (due to drain and diversion) from the vegetative parts by the developing fruit (7, 9). Because depodding (4) and deseeding (6) extend the life of soybean plants far beyond normal, the seeds must control monocarpic senescence in soybeans. For convenience, this influence of the seeds will be termed the senescence signal (6). In the soybean, the primary target of the senescence signal is the leaves (8).

The theories which hold that the senescence signal is a nutrient deficiency have been questioned some years ago (4, 9–11). Recently, it has been shown that, in surgically modified soybean plants, seed growth (with the accompanying nutrient drain and diversion) can occur without producing the senescence response (12) which raises doubts about the role of nutrient exhaustion in the induction of monocarpic senescence (9, 11). Nonetheless, where senescence does occur, important constituents, especially nitrogen, move out of the leaves, and this seems to be an important, even if secondary, component of the senescence of attached leaves (9, 10).

Photosynthates and other 'nutrients,' such as amino acids and hormones, being exported (withdrawn) from the leaf blade would have to travel down through the petiole via the phloem which is a living tissue (1, 2, 13). We decided to test the nutrient withdrawal hypothesis by killing a small segment of the petiole with steam (often called 'girdling' or 'ringing'). This does not interfere with the ability of the xylem (which is already dead at functional maturity) to supply water, nutrients, and hormones to the leaf blade.

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MATERIALS AND METHODS

Soybeans (*Glycine max* [L.] Merrill) cv. Anoka were grown as described (5). Foliar senescence and fruit development were measured quantitatively following the visual procedures outlined elsewhere (5). Leaf yellowing measured in the visual procedure reflects the decline of essential functions during monocarpic senescence of soybean (8). Increased fruit maturity index (FMI) represents greater maturity up to five (all pods brown). When the most advanced pods had reached full length (and width) and the seeds were just starting to grow, all pods were removed (depodded plants; Fig. 1B), or all except those at a single central node were plucked (single pod cluster plants; Fig. 1C). Thereafter, all pods over 1 cm long were removed from depodded nodes once per week. At the time the seed of the most advanced pod in a cluster nearly filled the seed cavity (mid podfill), a 1-cm zone on the petiole of a leaf in the middle of the plant was heated with a jet of steam for about 1 min (Fig. 1). During the treatment, the petiole was rotated and precautions were taken to protect the blade and stem from the heat. Immediately after heating, the treated area was enclosed with cellophane tape fastened to a splint to prevent bending. Bending of the petiole or desiccation of the plant will cause shriveling of the leaves with steam-treated petioles. In general, there was no sign of other heat damage to the plant and no indication that water conductivity was affected.

To demonstrate that the phloem was destroyed, some plants were steam treated at three points around a single pod cluster: on the petiole and on the stem above and below the pod cluster when seeds in the pods were in early development. As expected, this treatment prevented further seed growth, because it destroyed the phloem connections between the pods and all leaves, so photosynthates could not be transported to the seeds.

RESULTS AND DISCUSSION

Figure 2 shows that phloem destruction in the petiole of both podded and depodded plants does not alter their expected behavior, *i.e.* depodded plants remain green over a period of time and podded plants senesce. Although the leaves with a zone of dead phloem in their petioles follow a fairly normal yellowing pattern, they do tend to show more distinct green zones along their veins at an intermediate stage of yellowing. This development of green zones also occurs to a variable degree in Anoka leaves without phloem destruction and more consistently in some other soybean varieties, but in most cases, it is transient.

Destruction of the phloem in a segment of the petiole does not prevent the pods from inducing senescence of that leaf (Fig. 2). One interpretation of this result is that the steam treatment or the loss of the phloem connection induces the senescence of the leaf, *e.g.* blocks the movement of ABA or toxins out of the blade via the phloem. This possibility is eliminated by the observation that the steam treatment does not cause the leaf to senesce if the pods have been removed. Therefore, the pods, not the steam treatment

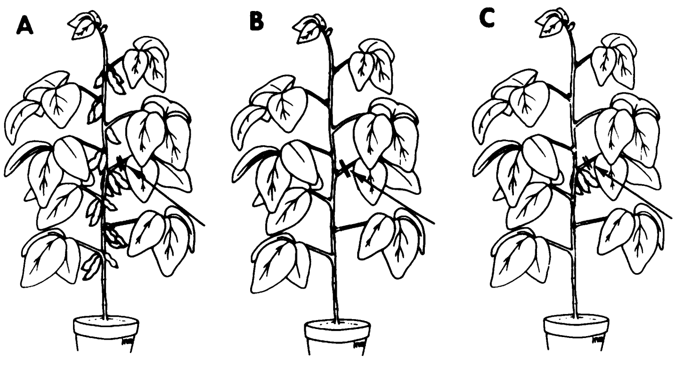

FIG. 1. Phloem destruction (steam) treatments (indicated by arrows) of soybean plants at mid podfill. A, Phloem destruction in the petiole of a leaf in the middle of a fully podded plant; B, same treatment of a plant completely depodded from the start of podfill and thereafter as the pods reached a length of 1 cm; C, same as B except that pods were allowed to develop only at a middle node (next to the leaf where the phloem was also destroyed).

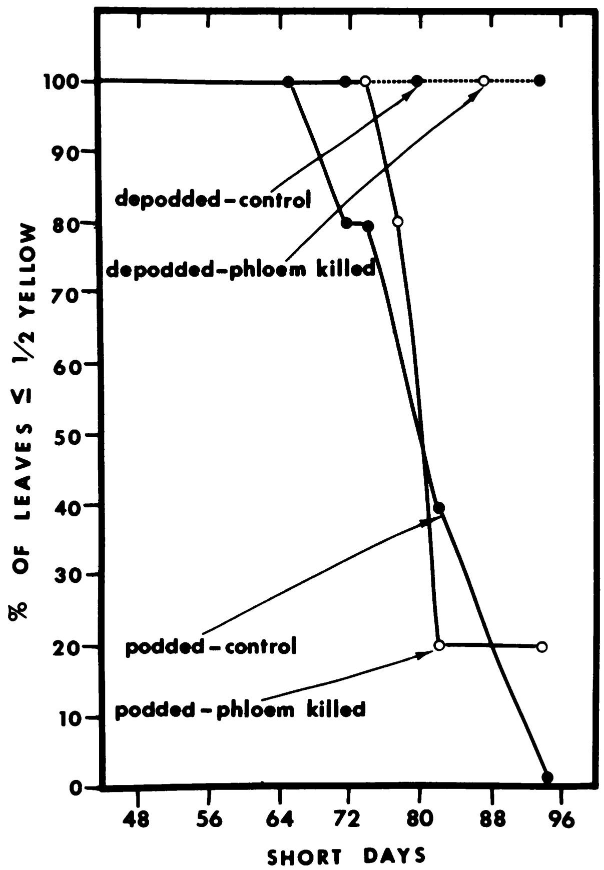

FIG. 2. Effect of phloem destruction in the petiole on senescence of leaves of depodded and podded soybean plants. The treated plants are shown in Figure 1, A and B.

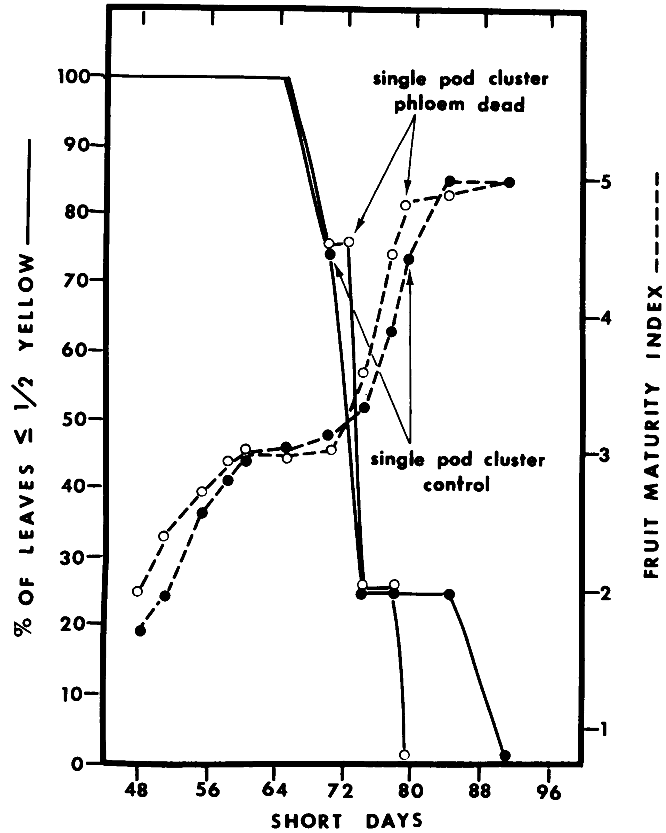

FIG. 3. Effect of petiole phloem destruction on pod development (fruit maturity index) and foliar senescence (in the leaf nearest the pods) in soybean plants with only a single pod cluster (see Fig. 1C).

Table I. *Effect of Phloem Destruction (Steam Treatment) and Depodding on the Nitrogen Content of Soybean Leaves*

Leaves of similar size and position (middle) on the plant were harvested from the control when these leaves turned yellow, and all the rest (1 week later) were harvested when the leaf next to the single pod cluster (with or without steam treatment in the petiole) was >½ yellow. Nitrogen was determined as described by Derman *et al.* (3).

Treatment	Total N/leaf
	mg
Control (with pods)	3.6
Depodded	18.5
Leaf next to single pod cluster (without steam treatment)	5.9
Leaf next to single pod cluster (with steam treatment of petiole)	17.0
Depodded (with steam treatment of petiole)	15.4

or disruption of the phloem, induce senescence.

Another interpretation of the data in Figure 2 is that the leaf with the steam-treated zone dies as an indirect result of the death of the rest of the plant. Because this is such a critical point, another type of test using single pod cluster plants was devised. When all pods are removed at an early stage, except those at a central node, the nearest (target) leaf senesces; however, most or all of the other leaves stay green and the plant remains alive (Fig. 3). Since phloem destruction does not prevent senescence of the leaf closest to the single pod cluster, the senescence of that leaf cannot be an indirect result of senescence of the rest of the plant. In addition, phloem destruction does not alter pod development (dry weight accumulation and the time course of the fruit maturity index) in the single pod cluster plants.

During the normal course of senescence in soybeans, nitrogen is transferred from the leaves to the seeds (3, 9). Destruction of the phloem in the petiole of the leaf next to the single pod cluster prevents the movement of nitrogen out of that leaf (Table I), even though it does not block Chl breakdown.

Since (a) nutrients would have to be withdrawn from the leaf via the phloem and (b) phloem destruction does not prevent the pods from inducing senescence in that leaf, our results virtually eliminate the theory that the seeds induce senescence of soybean leaves by withdrawing the nutrient resources in the leaves. Still, it must be recognized that mobilization of nutrients from leaves to the pods normally does occur, and this is considered an essential component of the senescence process (9, 10). Moreover, we have observed that detached soybean leaves or leaf discs yellow abnormally and very slowly, thereby suggesting a need for nutrient withdrawal. Thus, it is of considerable importance that senescence (here measured as yellowing) can proceed in attached soybean leaves without nutrient withdrawal. Even though the normal exodus of nitrogen via the petiole does not occur, some nitrogen could be lost through volatilization (14), but this loss does not seem to be very great here. The main mechanisms left are: the seeds (a) produce a senescence-inducing hormone(s) which travels up into the leaf with the xylem sap and (b) divert nutrients (or cytokinin) away from the leaves (9, 11). The nutrient (cytokinin) diversion idea is not consistent with other data which are discussed elsewhere (9, 11, 12). Whatever the nature of the senescence signal, it can be transmitted via the xylem to the leaves where it initiates breakdown of Chl and probably other leaf constituents leading to death.

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