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Short Communication

Photoperiodic Control of Apical Senescence in a Genetic Line of Peas[1]

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ABSTRACT

An early flowering genetic line of peas (*Pisum sativum* L.), designated G2, has dominant genes at two different loci, both of which function in short days to greatly extend the reproductive phase and thus to delay apical senescence. Long days (18 hours) promote senescence in this line, but the effect is reversible by reinstatement of short days (9 hours) until 3 to 4 days before the apex senesces. The response to photoperiod was quantitative. Increasing the photoperiod from 14 to 18 hours led to a progressive decrease in the number of nodes formed prior to death of the apex. Induction of senescence was determined by the total number of hours of light and darkness rather than by the length of the dark period. Senescence required flower and fruit development as well as long days.

Apical senescence is defined as those processes preceding the death of the apex, which, in monocarpic annuals, is inevitably followed by the death of the whole plant. An early flowering genetic line of peas, designated G2, is photodependent with respect to apical senescence (8). In long days, the plants fruit and subsequently senesce after a short reproductive phase. In short days, however, despite entering the reproductive phase, apical growth continues for a protracted period of time, and apical senescence does not occur. This behavior is dependent on the presence of dominant genes at two different loci. Recent evidence (10) indicates that the two loci in question are *Sn* and *Hr*, so these symbols will be employed here. Plants with recessive alleles at either one or both of the loci flower and senesce regardless of photoperiod.

In 1928, Molisch (9) observed that senescence could be deferred by hindering reproductive development, and proposed that the fruits served as nutrient sinks to exhaust the plant and prevent further growth. Leopold *et al.* (4) showed that fruits exerted their greatest promotion of leaf senescence not at the time of fruit growth, as would be expected if nutrient exhaustion were the prime factor, but at fruit maturation. Similar results have been noted with regard to apical senescence. Lockhart and Gottschall (5) found that removal of young fruits of Alaska peas enabled the shoot apex to grow for a longer period than if fruit maturation occurred on the plants. Even though shoot apices of Alaska peas failed to grow during fruit development, apical growth resumed provided the fruits were removed prior to ripening (7). In Greenfeast peas, only fruit maturation was found to alter the physiology of stock plants sufficiently such that grafted young apical buds failed to grow, and some senescence stimulus was suggested to be involved (6).

Since whole plant senescence is generally a consequence of reproductive development, it has hitherto been difficult to study the control of senescence alone. By the use of the G2 line, which flowers and fruits but fails to senesce in short days, senescence can be initiated by transferring a mature plant with fruits from short to long days. As the effect of fruits is included in any measurements made on mature plants in short days, whole plant senescence can be examined, unencumbered by the effects of fruiting, following transfer to long days. In this paper, we describe the environmental factors regulating apical senescence of G2, as a foundation for biochemical studies in progress.

MATERIALS AND METHODS

Seeds of pea (*Pisum sativum* L.) line G2 were planted singly in 15-cm clay pots filled with a mixture of sand, soil, and peat (1:1:1). Plants were fertilized every 2 weeks with a complete nutrient solution and the lateral branches were routinely trimmed. Most experiments were conducted in growth cabinets. Lighting was provided by fluorescent tubes supplemented with incandescent bulbs. The average full light intensity was 3400 $\mu w/cm^2$ at pot level. The standard short and long days were 9 and 18 hr, respectively, and day and night temperatures were 20 C and 15 C, respectively. Some experiments were performed in the greenhouse with supplemental lighting for 18 hr and the temperature maintained at similar levels. Low light intensities (< 100 $\mu w/cm^2$) in different spectral regions were used to extend a 9-hr period of high intensity light at 18 hr. Filters (red [823], blue [866], green [874] and far red [two red plus one blue filter]) (Edmund Scientific Co.) were fitted in the top of a light-tight box placed in the growth cabinet, under fluorescent light only for visible wave lengths, and under incandescent light only for far red illumination.

In all cases, the criteria for senescence of the shoot apex were a decrease in the size of the apical bud and rate of growth, and a loss of green coloration. "Senesced" is defined as the point at which growth of the shoot has ceased, close to the completion of the senescence process, but prior to the death of the apex. Once the apex has died, further growth cannot occur, yet a resumption of growth may occur at any phase of senescence prior to the death of the apex. Leaf senescence was not recorded, as most leaves were usually still healthy at the time the apex senesced. Leaf senescence has also been found to be unrelated to whole plant senescence (6). Node counts were used to measure re-

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sponses. The first reproductive node was the node at which the first flower bud was initiated, even if aborted.

RESULTS

Light Control. The number of long days required to induce senescence was determined by growing G2 plants in short days (9 hr) until anthesis of the first flower, which occurred at node 10 on the average. The plants were then subjected to a series of long day treatments and returned to short days. Senescence of the apex occurred after a minimum of 25 long days. The effect of long days on the G2 line was reversed by the restoration of short days, until 3 to 4 days before the appearance of the final node. The response to photoperiod was quantitative (Fig. 1). Under 9-hr photoperiods, growth was indeterminate. Plants subjected to intermediate day lengths (12–14 hr) lacked the robustness of plants in shorter days, but still exhibited an extended reproductive phase. With increasing day length, the number of reproductive nodes produced prior to apical senescence declined gradually to a minimum which was reached under the 18-hr photoperiod.

The senescence response of G2 was based on the total duration of illumination (or darkness) received per 24 hr (Table I). Interruption of a long dark period with 1.5-hr light break failed to induce senescence. Conversely, a break in the continuity of the light period also failed to affect the response, even though 2 short days were given per 24-hr period.

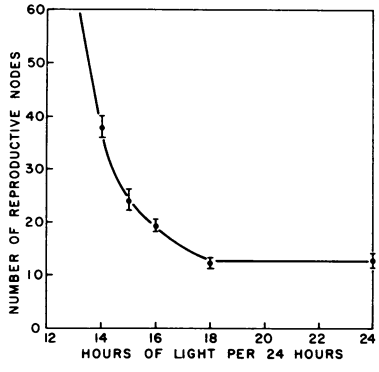

FIG. 1. Influence of photoperiod on the number of reproductive nodes produced by G2 peas prior to death of the apex.

The effect of light quality was examined by exposing the plants to 9 hr of full intensity white light followed by 9 hr of nonphotosynthetic intensity blue, green, red, or far red light. Senescence occurred in the blue, red, and far red treatments, but not in the green treatment. Plants in 18-hr white light produced 70 to 100% more reproductive nodes prior to senescence than the blue-, red-, or far red-treated plants, which had smaller leaves, lighter pigmentation, and longer internodes than the controls.

Fruit Requirement for Senescence. Under long days, the symptoms of senescence in the apex started with the initial development of the first fruits and increased to a maximum when these fruits had fully elongated. The senescence-promoting effect of the fruits appeared to decline thereafter, so that matured fruits did not contribute further to the senescence response. Removal of the fruits prior to maturity caused a resumption of growth. Defloration of G2 plants in long days prevented senescence indefinitely. Under these conditions, the newly formed internodes were shorter and the leaves were convoluted and darker green in color. Up to 90 reproductive nodes were produced before the experiment was terminated. The number of fruits required for apical senescence varied with day length, light quality, temperature, and nutrition. Under the glasshouse conditions previously described, various combinations of flowers were removed. An average of five fruits were required to cause senescence (Table II). The nondeflorated controls produced more fruits than the minimum number required for senescence. With fruit numbers near the minimum for the induction of senescence, apical growth resumed, in some cases, as the oldest fruits matured.

DISCUSSION

Whole plant senescence generally requires the previous development of reproductive structures (4–6, 9) and, therefore, is

Table I. Influence of Photoperiod on the Number of Reproductive Nodes Formed in G2 Peas Prior to Apical Death

The photoperiods were maintained from the time the plants were 14 days old until the plants senesced or until the termination of the experiment 120 days later.

Photoperiod Type	Light Regime Sequence Hours of: Light	Dark	Light	Dark	Total Hours Light per 24 hours	Total Hours Dark	Total Number of Reproductive Nodes
Short day	9	15	-	-	9	15	Indeterminate(>30)
Long day	18	6	-	-	18	6	12.1 ± 0.37
Short day & night break	9	8	1.5	5.5	10.5	13.5	Indeterminate(>30)
Long day & day break	9	1.5	7.5	6	16.5	7.5	12.1 ± 0.40
Long day as 2 short days	8	4	7	5	15	9	15.5 ± 0.48
Short day as 2 short days	9	4	3	8	12	12	Indeterminate(>30)

Table II. The Number of Fruit Required to Induce Apical Senescence in G2 Plants in Long Days

Includes only fruits in the post-petal fall and pre-maturity stages.

Treatment	Plants Senescing	Fruits at Senescence or Termination(±SE)	Senesced Apices that Restarted Growth	Restarts that Died
	%	No.		%
Control - no flower removal	100	8.2 ± 0.5	27.3	100
1 on: 1 off alternate flowers removed	72.7	5.0 ± 0.4	37.5	33.3
1 on: 2 off sequentially two-thirds of the flowers removed	25.0	4.7 ± 0.3	100	—
1 on: 3 off sequentially three-fourths of the flowers removed	0	3.7 ± 0.3*	--	--

* The total number of fruits, including those that were mature, was 6.6 ± 0.4.

dependent on photoperiod in plants where flowering is photoperiodically controlled. In many instances, endogenously controlled senescence will occur after a prolonged period of time with continuous defloration (5), although this has been found not to be the case in G2 peas over the experimental period tested. Krizek *et al.* (3) were able to induce the senescence of disbudded *Xanthium* plants in short days, under photoperiodic conditions that induced flowering in intact control plants. This indicated that although the stimulus for flower induction and senescence was similar, the two phenomena could be separated. In no case previously, however, has any investigation of whole plant senescence been carried out on plants in which senescence is photoperiodically controlled, even though flowering occurs regardless of photoperiod.

In G2, flowering is independent of photoperiod, although in short days, more flower buds abort than in long days. G2 requires continued long day conditions to induce senescence, and responds quantitatively to changing daylength and to the total duration of light or darkness received in a 24-hr period. Senescence was promoted by extending the daylength with low intensity blue, red, or far red light, whereas green light had no effect. In the liverwort *Marchantia,* senescence is enhanced by far red light and phytochrome has been shown to be the receptive pigment (1, 2). The blue, red, and far red treatments appeared to prevent the action of the *Sn* and *Hr* genes as indicated by the decrease in the number of reproductive nodes of the exposed plants, which is the distinguishing criterion for the presence or absence of these genes.

Fruit development combined with long days are required for senescence to occur. The removal of flowers or fruits in long days prevented the cessation of growth indefinitely. In G2, the apex senesced at about the time that the oldest fruits finished elongation, indicating that the senescence stimulus was present early in fruit development prior to seed enlargement. Removal of fruits prior to maturation, however, allowed growth to resume, indicating that these fruits still inhibited apical growth and that the senesced apex was not dead at that point. In G2, it is clear that nutrient exhaustion is not the cause of senescence. The process of apical senescence is induced in G2 and related lines prior to fruit filling, the phase of greatest nutrient demand, and in short days, G2 develops a very large quantity of fruit without developing any evident symptoms of senescence.

A critial number of fruits was required to cause apical senescence. The determining factor was the number of developing fruits prior to maturity present at any one time. It appeared that mature fruits did not continue to produce the senescence factor, and that with partial fruit removal, the stimulus provided by the remaining fruits was insufficient to prevent growth, so that apical growth resumed if the apex had not died. The new flush of growth continued until the minimum number of fruits required to induce senescence was again reached or exceeded. This recrudescence showed that senescence is not synonymous with death, although senescence precedes death of the apex. In the nondeflorated controls, by the time the minimum number of fruits was present, other young fruits were also developing and these matured even though the apex had senesced.

Our experiments indicate that both long days and the presence of fruits are required together to induce apical senescence in G2 peas. Senescence responds quantitatively to photoperiod, but the response to low light intensity suggests that the phenomenon of photodependent apical senescence is not a photosynthetic response. We are presently investigating the involvement of plant hormones.

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