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Photoperiodic and Genetic Control of Carbon Partitioning in Peas and Its Relationship to Apical Senescence[1]

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ABSTRACT

Apical senescence but not flower initiation is delayed by short days (SD) compared to long days (LD) in pea plants (*Pisum sativum* L.) of genotype *E Sn Hr*. We recently reported that delay of senescence correlated with slower reproductive development, suggesting that fruits are weaker sinks for assimilates under delayed senescence conditions. Thus, we have examined assimilate partitioning in peas to determine if genotype and photoperiod regulate relative sink strength. Assimilate diversion by developing fruit has been implicated in senescence induction. A greater percentage of leaf-exported ^{14}C was transported to fruits and a smaller percentage to the apical bud of G2 peas (genotype *E Sn Hr*) in LD than in SD. Relatively more of the ^{14}C delivered to the apical bud of G2 peas was transported to flower buds than to young leaves in LD as compared to SD. There was no striking photoperiodic difference in carbon partitioning in genetic lines without the *Sn Hr* allele combination. The *Sn Hr* allele combination and photoperiod may regulate the relative strength of reproductive and vegetative sinks. Photoperiodic differences in sink strength early in reproduction suggest that these genes regulate sink strength by affecting the physiology of the whole plant. High vegetative sink strength in SD may maintain assimilate supply to the apical bud, delaying senescence.

Monocarpic plants senesce after a short reproductive phase. Senescence can be delayed if the vegetative phase is extended by manipulation of the photoperiod or if the developing reproductive structures are continually removed (19). The latter observation led to the assignment to the reproductive structures of a central, causal role in senescence (25). Historically, it has been hypothesized that the reproductive structures induce senescence either by depleting the resources of the rest of the plant due to their strong sink strength (16), or by exporting a senescence hormone (13).

The G2 line (genotype *E Sn Hr*) of peas has been considered to be evidence antithetical to the nutrient drain hypothesis (6, 14). In lines with the *E Sn* allele combination, plants initiate flowers at the same node regardless of the photoperiod, but apical senescence is delayed in SD[2] compared to LD (17). The *Hr* allele magnifies the effects of these alleles, and G2 peas do not senesce in SD (9 h photoperiod) under our growing conditions. Thus, in this line, senescence does not occur in SD despite fruit production and the accompanying nutrient drain to the fruits, which may be as great under nonsenescing as under senescing conditions (6). However, we recently demonstrated that the rate of reproductive development, as well as senescence, is regulated by the interaction of these genes and photoperiod (11). The rate of reproductive development, compared to the rate of node production, is slower in SD than in LD. Thus, the nutrient drain by fruits from each leaf may be less in SD than in LD. This led us to hypothesize that the delay of senescence in SD is due to reduced demand of the developing reproductive structures for assimilates, resulting in more assimilates available for vegetative growth. The *Sn* allele in the presence of the *Hr* allele may indirectly regulate senescence via direct effects on the relative strengths of the reproductive and vegetative sinks.

To test the above hypothesis, we have measured the relative strength of the reproductive and vegetative sinks in pea plants with different genotypes and grown in different photoperiods.

MATERIALS AND METHODS

Plant Material. Pea plants (*Pisum sativum* L.) of the following genetic lines, described by Murfet and Marx (18), were used in this study: line I3 (tall phenotype, genotype *e sn hr*), line I2 (dwarf phenotype, genotype *E Sn hr*; this genetic line exhibits weak expression of the *Sn* allele compared to other genetic lines), and line G2 (dwarf phenotype, genotype *E Sn Hr*). All of these genetic lines are photoperiodically insensitive with respect to flowering node.

Plant Growth. Seeds were sown singly in 15 cm clay or plastic pots in a mixture of peat and vermiculite (1:1 v/v) in a greenhouse at 20 ± 5°C. Nodules formed under these growth conditions. Plants were watered daily after emergence, and beginning 3 weeks after sowing were supplied weekly with a complete nutrient solution (20:20:20) until transfer to growth chambers which took place at least 2 weeks before expansion of the first flowering node. Standard photoperiods in the growth chambers were 9 h light/15 h dark (SD) and 18 h light/6 h dark (LD) every 24 h. Lighting was provided by a mixture of fluorescent and incandescent lamps for an average irradiance of 250 μmol photons $m^{-2} s^{-1}$ at pot level to 550 μmol photons $m^{-2} s^{-1}$ at maximum plant height. Growth chamber temperatures were 17°C during the dark period and 19°C during the light period. Plants were watered daily with a dilute complete nutrient solution. Lateral branches and second flowers at a node were routinely removed if they developed.

Partitioning Studies. Plants were treated just prior to expansion of the youngest leaf out of the apical bud, the stage described as 0.5 by Maurer *et al.* (15), or as close to this stage as possible. All plants were treated at a developmental stage prior to the visual symptoms of apical senescence. Treatments were made 3 to 4 h into the light period to plants with the specified number of reproductive structures. With the exception of G2 peas grown in SD, plants had the same number of reproductive nodes and reproductive structures. G2 plants grown in SD often had more reproductive nodes than reproductive structures due to the abortion of some of the reproductive structures. However, plants were selected with apparently vigorous (nonabortive) reproduc-

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[2] Abbreviations: SD, short days; LD, long day.

tive structures in the upper nodes so that the complement and arrangement of reproductive structures was the same for all genotypes within one treatment.

Whole Plant Partitioning. Pea plants of line I3 or G2 grown in SD and LD were treated in a fume hood under laboratory lights when they had five or six reproductive nodes, respectively. In order to treat each line at a comparable developmental state, line I3 plants were treated when they had fewer reproductive nodes than G2 peas as they produce fewer total nodes than G2 peas. One of the leaves at the third through sixth node from the apical bud was enclosed in a 10 × 15 cm plastic bag. A 3 ml plastic beaker was affixed to the inside of the plastic bag before sealing. The bag was affixed with adhesive tape around the petiole to form a gas-tight seal. 20 nmol of $NaH^{14}CO_3$ or $Na_2{}^{14}CO_3$ (specific activity 50 mCi $mmol^{-1}$) in 25 μl H_2O was injected into the beaker through the plastic. This was followed immediately with an injection of 100 μl of 0.3 N HCl into the beaker to liberate $^{14}CO_2$. The puncture was sealed with tape to form an airtight seal. Plants were transferred back to the growth chambers within 15 min after removal. The bag was left in place for 1 h. Five to 6 h after initial exposure to $^{14}Co_2$, plant parts of interest were excised, weighed, and stored within 30 min of excision at −80°C at least overnight. Samples were oven-dried at 50°C for approximately 24 h, oxidized in a Packard sample oxidizer, and the collected $^{14}CO_2$ counted in a liquid scintillation counter. The entire shoot, minus the excised parts and the treated leaf, was ground to near-homogeneity after freezing and drying as described above. Aliquots were combusted and assayed to provide an estimate of the total ^{14}C exported to the shoot from the treated leaf. Data represent the mean of three plants. Experiments with ^{14}C-sucrose yielded similar results.

Partitioning Within Apical Bud. For partitioning studies within the apical bud, the fourth leaf from the apical bud of lines I2 or G2 grown in SD or LD was treated when the plant had four reproductive structures. Leaflet surfaces were gently abraded with carborundum and washed with distilled H_2O. A 6.5 mm-diameter ring of nylon tubing was affixed to the abraded leaf surface with stopcock grease. Approximately 1 nmol of [U-^{14}C]sucrose (specific activity 584 mCi $mmol^{-1}$) in 30 μl of 1% Tween 20 was pipetted into the ring. The ring was covered with a glass cover slip to prevent evaporation. Flower buds and young leaves at the two most mature nodes still contained within the apical bud were dissected out of the apical bud with forceps 5 to 6 h after treatment. Samples were weighed, frozen, dried, and analyzed as described above.

Data for line G2 represent the mean of three or five replicates and, for line I2, five to six replicates. The experiment was replicated with older plants, with similar results.

RESULTS

Transport of carbon from leaves was essentially restricted in this study to the same side of the plant as the treated leaf, as only low amounts of ^{14}C were recovered from reproductive structures on the side of the plant opposite the treated leaf (data not shown). This is consistent with the vasculature, as leaves of pea plants do not have direct vascular connections with fruits on the opposite side of the plant (20). Leaves mentioned below are in reference to their location, in number of nodes, from the apical bud.

Whole Plant Partitioning. Over the 5 to 6 h transport period, greater percentages of the labeled assimilates were exported from the leaves to the shoots of the G2 pea plants grown in LD than in SD (36.6 ± 7.6% *versus* 13.6 ± 1.5%, respectively, for the sixth leaf from the apical bud).

In all cases except for G2 pea plants grown in SD, greater percentages of the ^{14}C exported from the treated leaf were transported to the axillary fruit as the distance between the treated leaf and the apical bud increased, and, therefore, as the age and size of the reproductive structure increased (Fig. 1). For G2 plants grown in SD, the percentage of ^{14}C exported from the third to sixth leaves which was transported to the reproductive structure in the axil of the treated leaf was not significantly affected by node position or age of the reproductive structure (Fig. 1).

The percentage of the total ^{14}C exported from leaves four to six which was transported to the axillary fruit of line G2 was greater in LD than in SD (Fig. 1). The cumulative transport to all reproductive structures on the same side of the plant as the treated leaf was two to four times greater in LD than in SD (Table I). For line I3 plants, similar percentages of the ^{14}C exported from leaves three and four were transported to the axillary fruit in both photoperiods. Less of the ^{14}C exported from the fifth leaf was transported to the axillary fruit in SD than in LD, but this difference was less than the differences between SD and LD detected in line G2 pea (17 *versus* 35%) (Fig. 1). There were no significant differences in the cumulative transport to all fruits on the same side of the plant as the treated leaf of line I3 whether they were grown in SD or LD (Table II).

In all cases, the greatest percentage of the ^{14}C exported was transported to the apical bud when the fourth leaf was treated. This is consistent with the vasculature of pea plants, as the most mature new leaf within the apical bud has direct vascular connections with the fourth and sixth, but not third or fifth, leaves (20). The third leaf exported primarily to the first leaf (data not shown) while the second leaf had not yet fully developed export capacity (2).

A greater percentage of the total ^{14}C exported from leaves three to six was transported to the apical bud of line G2 grown

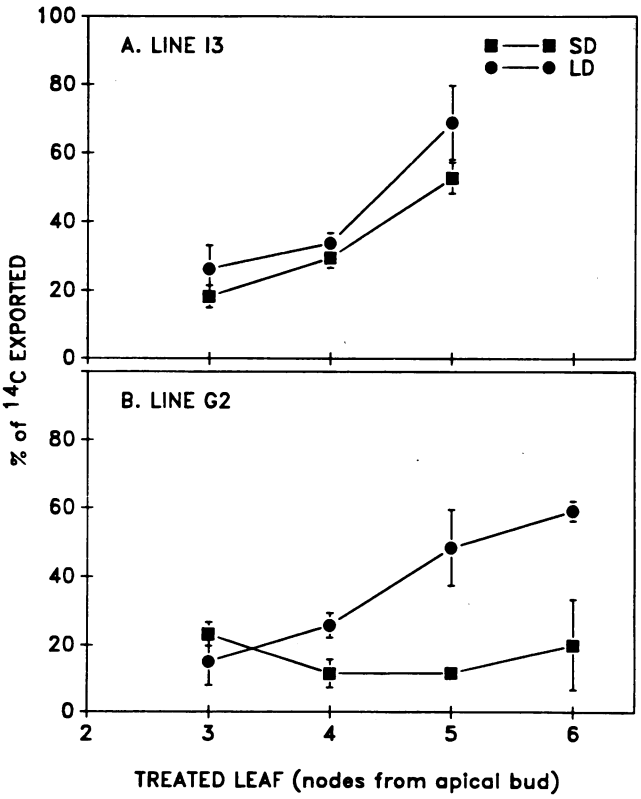

FIG. 1. Percent of assimilated ^{14}C transported to the reproductive structures of A, line I3 and B, line G2 peas. The percentage of ^{14}C exported from leaves at the designated nodes that was recovered in the reproductive structure in the axil of the treated leaf 5 to 6 h after exposure of the leaf to $^{14}CO_2$.

Table I. *Percentage of ^{14}C Exported from Leaves of Line G2 Peas which Was Recovered in Reproductive Structures Above, At, or Below Axil of Treated Leaf 5 to 6 h after Exposure of Leaf to $^{14}CO_2$*

Conditions as in Figure 1.

	Treated Leaf (nodes from apical bud)							
	SD				LD			
	3	4	5	6	3	4	5	6
% to fruit above axil	2.2 ± 0.4[a]	6.3 ± 3.0	0.0 ± 0.0	0.1 ± 0.1	4.5 ± 1.8	6.2 ± 3.2	0.6 ± 0.4	6.0 ± 1.9
% to fruit in axil	23.3 ± 3.5	11.5 ± 4.2	11.7 ± 1.1	20.2 ± 13.4	15.1 ± 7.2	25.9 ± 3.6	48.6 ± 11.0	59.2 ± 2.9
% to fruit below axil	1.2 ± 0.6	5.2 ± 4.0	—[b]	—	9.9 ± 6.4	23.4 ± 2.0	—	—
Total	26.7 ± 4.5	23.0 ± 11.2	11.7 ± 1.1	20.3 ± 13.5	29.5 ± 15.4	55.5 ± 8.8	49.2 ± 11.4	65.2 ± 4.8

[a] ± SE of the mean (n = 3). [b] Plants did not have reproductive structures at this node.

Table II. *Percentage of ^{14}C Exported from Leaves of Line I3 Peas which Was Recovered in Reproductive Structures Above, At, or Below Axil of Treated Leaf 5 to 6 h after Exposure of Leaf to $^{14}CO_2$*

Conditions as in Figure 1.

	Treated Leaf (nodes from apical bud)					
	SD			LD		
	3	4	5	3	4	5
% to fruit above axil	4.0 ± 1.1[a]	5.7 ± 2.5	0.1 ± 0.0	3.8 ± 1.0	3.0 ± 0.8	0.0 ± 0.0
% to fruit in axil	18.3 ± 3.2	29.5 ± 2.9	52.8 ± 4.5	26.3 ± 6.8	33.8 ± 2.9	68.9 ± 10.8
% to fruit below axil	0.3 ± 0.1	—[b]	—	0.2 ± 0.1	—	—
Total	22.6 ± 4.4	35.2 ± 5.4	52.9 ± 4.5	30.3 ± 7.9	36.8 ± 3.7	68.9 ± 10.8

[a] ± SE of the mean (n = 3). [b] Plants did not have reproductive structures at this node.

in SD than in LD whether measured on a per bud or per weight basis (Figs. 2B and 3). The percentages of ^{14}C exported from leaves three to five which were transported to the apical bud of line I3 plants were similar in SD and LD, and similar to line G2 in LD (Fig. 2A).

In G2 peas, the fresh weight of the apical buds was similar in SD and LD at this stage of reproductive development, but the weight of the reproductive structure was less in SD than in LD

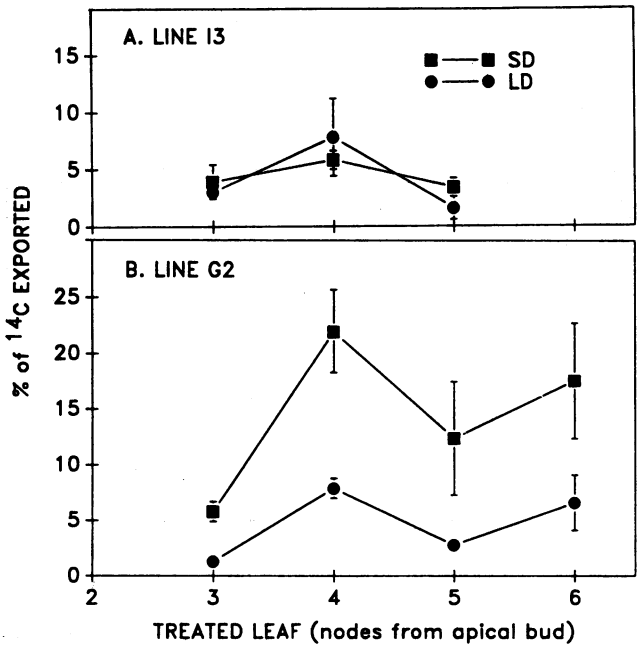

FIG. 2. Percent of assimilated ^{14}C transported to the apical bud of A, line I3 and B, line G2 peas. The percentage of ^{14}C exported from leaves at the designated nodes that was recovered in the apical bud 5 to 6 h after exposure of the leaf to $^{14}CO_2$.

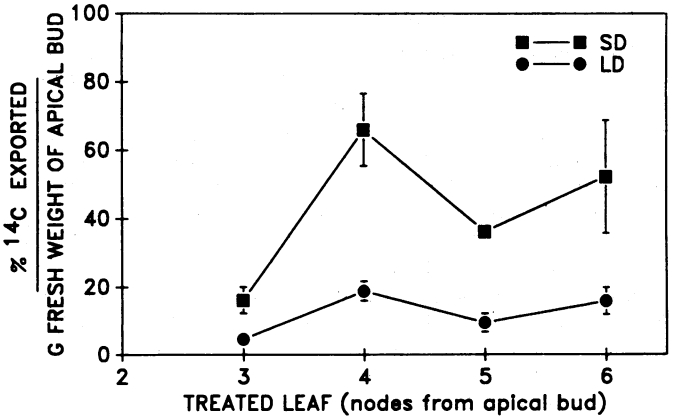

FIG. 3. Percent of assimilated ^{14}C transported to the apical bud of G2 peas per g fresh weight of bud. The percentage of ^{14}C exported from leaves at the designated nodes of G2 pea plants that was recovered in the apical bud, per g fresh weight of the bud, 5 to 6 h after exposure of the leaf to $^{14}CO_2$.

(0.25 + 0.02 g *versus* 0.42 + 0.02 g for the axillary fruit of the fourth leaf). In one comparison of line I3 peas, these weights were not significantly different between SD and LD. In a second comparison, the fresh weight of the apical bud and reproductive structure were both less in SD than LD, but proportionally similar in both photoperiods (data not shown).

Partitioning Within Apical Bud. Plants were treated with [^{14}C]sucrose at the fourth leaf from the apical bud as this was the principal leaf supplying photosynthate to the apical bud. Line I2 (genotype *E Sn hr*) was used as a control for line G2 since the apical bud of line I3 peas is too small to easily dissect. Line I2 exhibits only weak expression of the *Sn* allele. The data are expressed as the ratio of the dpm recovered from the flower buds to the dpm recovered from the young leaves within the apical bud. (These ratios would be the same whether derived from dpm values or from the percent of the total amount of ^{14}C exported

from the treated leaf.) Nine times more ^{14}C was transported to the flower buds relative to the young leaves of G2 pea plants grown in LD than in SD (Table III). The distribution of ^{14}C between the flower buds and young leaves within the apical bud of line I2 was not significantly different between SD and LD, although the mean was greater in LD (Table III). These ratios were similar between line I2 and line G2 grown in LD.

DISCUSSION

Partitioning and Relative Sink Strength in Peas. Sink strength has been defined as the capacity of a sink to take up assimilates (26). The method of measurement of sink strength used in this study determines the distribution of assimilates exported from a single leaf (assuming that 3–4 h into the photoperiod distribution between sinks has reached a steady state). These data can be interpreted in terms of relative sink strength but provide no information on the actual amount of carbohydrate taken up by the sinks. However, measurements of net photosynthetic rate of G2 peas revealed no striking photoperiodic difference (10). Photosynthetic period also had little effect on the photosynthetic rate of soybean leaves (3). Export of assimilated ^{14}C (during the light period) was less in SD than in LD in G2 peas. This has also been demonstrated to be an effect of shortened photosynthetic period for soybean (3). The stored carbohydrate is apparently exported during the long dark period (3, 8). Similar photosynthetic rates and reduced leaf export in SD compared to LD indicate that fewer total assimilates are exported from the leaves of G2 peas in SD during the time period of this study. Thus, since photosynthetic period appears not to affect the rate of respiration (8), a higher percentage of the assimilates exported may be lost through respiration from plants in SD than in LD. A greater net loss in SD than LD should not affect the relative distribution, but disproportionate losses from the different sinks would represent a source of error. The slow rate of growth of fruit of G2 peas in SD (11) may be accompanied by a slow rate of respiration; this would underestimate the differences we have detected in this genetic line.

Empirical measurements of sink strength in a competitive situation are dependent on a number of factors, not all of which are sink properties. Other influencing factors, such as age, number of sinks, and growing conditions were controlled in this study to validate comparisons of relative sink strength between plants within a treatment. To determine true photoperiodic differences in the G2 line, the variable of photosynthetic period was controlled by determining its effects on partitioning in photoperiodically insensitive lines. This control was used as night breaks of light are ineffective in changing the photoperiodic response of G2 peas (21).

Developing fruits of line G2 grown in LD and of line I3 grown in both photoperiods were strong sinks for assimilate from their subtended leaves since they received a large proportion of the exported carbon, as has been noted previously for peas (20). Fruit sink strength increased with fruit maturity, which is expected since fruit weight increased with age and maturity. Fruits were stronger sinks for assimilates from their subtending leaves than was the apical bud. In contrast, young fruits of G2 peas grown in SD had nearly equal sink strength for assimilates from their subtending leaves as did the apical bud. Young fruits of plants of line G2 in SD cannot be considered to be strong sinks for leaf-exported assimilates as they did not receive a large proportion of these assimilates.

Young leaves within the apical bud were stronger sinks for assimilates from the fourth leaf than were the flower buds in all genetic lines and photoperiods. The relative sink strength of these structures were similar in G2 peas grown in LD and in line I2 regardless of the photoperiod, although the flower buds of line I2 grown in LD may have been slightly stronger sinks than they were in SD. The flower buds of G2 peas grown in SD had much weaker sink strength relative to the young leaves than they did in LD.

Failure to detect a striking photoperiodic difference in the relative strength of the reproductive and vegetative sinks of line I3, which is photoperiodically insensitive, suggests that partitioning patterns are not markedly altered in peas in response to photosynthetic period. This is consistent with our finding that the rates of growth of these sinks are affected to the same degree by changes in the length of the photosynthetic period (11). The similar partitioning of exported assimilates is also in complete agreement with the results of Hole and Scott (9), who found that dry matter partitioning in peas was independent of the total assimilates in the plant (although total assimilates may influence vigor and size of plant parts and, therefore, sink strength indirectly). On the other hand, there was a trend for increased partitioning to reproductive sinks relative to vegetative sinks in LD compared to SD in both lines I2 and I3. Because of the weak expression of the *Sn* allele in line I2, it is likely that any effects of the *Sn* allele on partitioning would not be detectable in this line, and cannot be identified from these data. However, the differences observed in partitioning between vegetative and reproductive sinks of G2 peas grown in SD and LD may be truly photoperiodic and attributable to the *Sn* allele in the presence of the magnifying effect of *Hr*, since the *Sn* allele confers photoperiodic sensitivity to peas (17) and since these large differences were not detected in lines I2 and I3. We conclude, therefore, that the relative strength of the reproductive and vegetative sinks of pea plants are regulated by photoperiod and gentoype. The *Sn Hr* allele combination and SD may decrease the strength of the reproductive sinks relative to the strength of the vegetative sinks.

As fewer total assimilates were exported from the leaves in SD than in LD during the light period, it seems likely that the fruits of G2 peas grown in SD received fewer total assimilates as well as a lower percentage of the exported assimilates than did the fruits in LD. Whether the apical bud received more total assimilates as well as a higher percentage in SD than in LD is not as easily ascertained. However, our data indicate that of the

Table III. *^{14}C Partitioning between Young Leaves and Flower Buds within Apical Bud of Lines G2 and I2 Peas 5 to 6 h after Treatment of Fourth Leaf with [^{14}C]Sucrose*

Plants were treated during the photoperiod at a time when they had 4 nodes with reproductive structures.

	Genotype and Photoperiod			
	Line G2		Line I2	
	SD	LD	SD	ID
$\frac{\text{dpm in flower buds}}{\text{dpm in young leaves}}$	0.04 ± 0.03[a]	0.35 ± 0.08	0.28 ± 0.07	0.45 ± 0.19

[a] ± SE of the mean (n = 3–6).

assimilates delivered to the apical bud, a very small percentage are delivered to flower buds in SD, while this percentage is considerable in LD (Table III). Furthermore, we have demonstrated that as plants in LD develop, more mature reproductive structures will be borne in the axils of the top leaves. The resources of upper leaves may become more committed to their subtended fruits (which were stronger sinks than were the flowers), and partition fewer of their resources to the apical bud. In contrast, the fruit on the plant in SD remain four to five nodes from the apical bud (11) as the plant matures. Thus, the photoperiodic differences in assimilate allocation identified in this study may become more pronounced as the plants age.

The relative sink strength of pea plants may be regulated, at least in part, by the gibberellin content of the shoot (5).

Role of Assimilate Partitioning in Apical Senescence of Peas. A nutritional basis to senescence of monocarpic plants was envisioned by Molisch (16), who suggested that fruits or seeds divert assimilates from the vegetative plant, triggering senescence of the vegetative plant when it receives insufficient assimilates to survive. The correlation of delayed apical senescence and greater assimilate supply to vegetative structures demonstrated here support some aspects of Molisch's proposal (16). Both the nutrient drain hypothesis and a hypothesis in which it is proposed that the reproductive structures produce and export a senescence signal (19), assign a central, senescence-inducing role to fruits or seeds, no doubt due to the observation that removal of reproductive structures delays or prevents senescence of many species (19). However, senescence of peas (22) as well as other species (19) has been reported in the absence of fruits, and argues against a central, inducing role for fruits and seeds in senescence. In soybean, early senescence-like changes and loss of assimilatory capacity were independent of the presence of fruit (1, 4). The authors of these reports speculated that senescence was induced early in the reproductive phase, and was only enhanced by the fruit. Our results are consistent with this conclusion. The effects of the senescence-controlling genes were apparent on assimilate partitioning within the apical bud of G2 peas, long before fruits or seeds were present. It seems likely that these genes mediate partitioning between primordia, very early in reproductive development.

In line with our conclusions, Reid and Murfet (23) have also suggested that the effect of the *Sn* allele and its modifying genes may be to "direct the resources of the plant towards particular ends." These conclusions were drawn from studies of pea plants lacking the genetic potential to initiate flowers. In these lines, decreases in the rate of plant growth occurred at about the same time that they did in normal plants in the same phenotypic class, early in the reproductive phase of the flowering plants. The effects of the *Sn* allele and photoperiod on apical senescence were still apparent in plants without the capacity to initiate flowers. Thus, relative sink strength may be a property of the whole plant and not dependent solely on the nature of the reproductive structures, although fruit properties clearly regulate assimilate uptake in the immediate sense (7). Root growth (24) and assimilation by roots (12) decline before the period of rapid pod growth in pea, indicative of a decline in the sink strength of the vegetative plant which is associated with flowering but apparently not attributable to strong reproductive sink strength only. While the ability of reproductive sinks to divert assimilates regulates senescence, we suggest that this ability is conferred on reproductive sinks by, and regulated by, the whole plant, starting early in the reproductive phase.

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