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Photoperiod gene control over partitioning between reproductive and vegetative growth*

D. H. Wallace[1], K. S. Yourstone[2], P. N. Masaya[3], and R. W. Zobel[4]

[1] Department of Plant Breeding and Biometry, Cornell University, Ithaca, NY 14853, USA
[2] Department of Fruit and Vegetable Sciences, Cornell University, Ithaca, NY, USA
[3] Instituto de Ciencia y Tecnologia Agricolas, Guatemala City, Guatemala
[4] USDA-ARS, Department of Soil, Crop and Atmospheric Sciences, Cornell University, Ithaca, NY, USA

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Summary. The hypothesis tested was that lack of photoperiod gene activity allows inherent partitioning of photosynthate to continued growth of the earliest potential buds, flowers, pods, and seeds (the organs that give rise to the yield). Alternatively, and competitively, photoperiod gene activity causes the photosynthate to be partitioned predominantly toward continued growth of new vegetative organs plus later initiation of more reproductive (yield) organs. This hypothesis was tested by comparing an insensitive and a photoperiod-sensitive bean (*Phaseolus vulgaris* L.) cultivar and their F_1 with F_2 segregates of undetermined genotype. Randomly derived homozygous F_8 segregates were also compared. The F_8 generation included one photoperiod-insensitive and one photoperiod-sensitive genotype in a 1:1 ratio, which verified control by one photoperiod gene. Under long daylength (LD), in addition to early versus late flowering and maturity, the two genotypes expressed opposite levels of 23 other traits that would be changed by competitive partitioning of the photosynthate. In contrast, under short daylength (SD), both genotypes flowered and matured early, and both expressed the levels for all 25 traits that the photoperiod-insensitive genotype expressed in both SD and LD. The photoperiod gene interacted with daylength to control the levels of all three major physiological components of yield: the aerial biomass, harvest index, and days to maturity. Included among the other traits with levels altered by daylength-modulated photoperiod gene activity were: the number of branches, nodes, leaves and leaf area, the rate of yield accumulation, and sink activity.

Key words: Sink – Sink activity – Source – Harvest index – Crop adaptation – Yield physiology – Maturity

Introduction

In 1967 the early, yelloweye class, dry bean cv 'Charlottetown' was crossed with the late, red kidney class cv 'Redkote'. The goal was the 50% gain in yield achievable if the higher harvest index of the early parent was combined with the larger aerial biomass of the late parent. The cross gave red-kidney cv 'Redkloud', which inherited both earliness and high harvest index. 'Redkloud' accumulates the same average yield in 85 days as 'Redkote' does in 105 days by partitioning a higher proportion of its biomass to reproductive organs (Bravo 1975; Kueneman 1978; Kueneman et al. 1979; Scully and Wallace 1990). 'Redkloud' is photoperiod insensitive, while the flowering and maturity of 'Redkote' are delayed by long daylength (LD) (Masaya 1978; Wallace and Enriquez 1980; Muhammad 1983; Gniffke 1985).

A higher temperature amplifies the delay in flowering due to LD (Wallace and Enriquez 1980; Wallace et al. 1991; Hodges 1991; Squire 1990). Higher temperature also causes each node to develop in fewer days, thereby simultaneously tending to cause earlier flowering.

Daylength and temperature alter yield by modulating the time the cultivar requires to develop to maturity (Hodges 1991; Squire 1990). Achieving a cultivar's full yield potential requires its genotype and the environment to give a genotype × environment interaction that results in a days-to-harvest maturity

* Department of Plant Breeding and Biometry paper no. 758
Correspondence to: D. H. Wallace

that is neither shorter nor longer than the growing season duration.

The objective of the investigation reported here was to elucidate effects by photoperiod gene activity on the physiological components of yield. Progeny from crosses between 'Redkloud' and 'Redkote' were used to elucidate these effects and to determine inheritance of the photoperiod sensitivity.

Materials and methods

F_1, F_2, and F_3 comparisons with the parents

'Redkloud' and 'Redkote' and their F_1, F_2, and F_3 progenies were compared in the field at Ithaca, New York under the LD of the summers of 1976 and 1977 (Masaya 1978). Masaya also compared them under both SD and LD in the growth chambers described below for comparison of the F_8 progenies. For each plant Masaya recorded days to first flower (DTFF) and the nodal position of that flower.

The F_1 and F_2 generations were expected to reveal and the F_3 to verify inheritance of the photoperiod response. However, as detailed in the results, the four environments each gave an apparently different F_2 segregation ratio for DTFF and a different distribution of nodal position of the first flower. Alteration of the segregation ratio by each environment resulted in inconclusive interpretations about inheritance.

After also experiencing inconclusiveness for inheritance of photoperiod response with early generations from other bean crosses, Gniffke (1982) suggested the use of F_8 progenies. Unselected F_2 plants were advanced under SD via single seed descent to the F_8 generation. Seeds harvested from the F_8 plants were then used to conduct tests in multiple environments using replicated experimental designs. Homozygosity at the F_8 generation eliminated variation due to ongoing segregation of the genotypes leaving only variation due to the homozygous genotypes, environmental differences, and the genotype × environment interaction of the segregates with the homozygous genotype.

F_8 experiment 1. Flowering phenotypes under long daylength

On July 3, 1986, 89 'Redkloud' × 'Redkote' F_8 progenies were planted in a ventilated greenhouse at Ithaca. Each F_8 was represented by 6 plants, 2 in each of three 20-cm pots. Also included were 12 pots of 'Redkloud' and 12 of 'Redkote'. Natural daylength was near 16 h at planting. Day temperature varied from a near-outside air temperature on cloudy days to one about 10 °C higher on sunny days. A summer-time greenhouse was used because high temperature combined with LD maximizes photoperiod gene activity (Wallace and Enriquez 1980; Muhammad 1983; Wallace et al. 1991). Recorded for each plant was its days (from planting) to a first flower (hereafter termed DTFF) and whether this flower was in the axil of the terminal leaf on the main stem, on the inflorescence arising from this axil, on a later developed primary branch, or on a yet later secondary branch.

F_8 experiment 2. Verification of photoperiod gene activity

Seventeen randomly selected F_8 progenies which in the LD greenhouse (Exp. 1) had expressed early flowering and photoperiod insensitivity and 17 that had expressed late flowering due to photoperiod sensitivity, plus the parents 'Redkloud' and 'Redkote', were planted in the greenhouse on November 25, 1986. Each progeny was represented by 4 plants (2 in each of two 20-cm pots). Natural daylength was near 9.6 h.

F_8 experiment 3. Photoperiod gene activity in controlled environments

Two F_8 progenies classified in the LD greenhouse (Exp. 1) as early flowering and photoperiod insensitive and two classified as late and sensitive, plus 'Redkloud' and 'Redkote', were planted in one growth-chamber with 11-h daylength (SD) and in another with 16-h daylength (LD). Under both SD and LD 5 plants of each parent and F_8 progeny were grown. Each plant was in a 20-cm pot. For this and the following (Exp. 4) growth chamber study, the number of flower buds at the terminal inflorescence of the main stem was recorded at the time of anthesis of the insensitive genotype for each plant of both the insensitive and sensitive genotype. Also recorded was whether the size of these buds was small or large. All growth chambers had 12/12-h, 26/18 °C day/night temperatures.

F_8 experiment 4. Test of partitioning in a controlled LD environment

Nine F_8 progenies previously classified in the LD greenhouse as photoperiod insensitive, 4 progenies classified as photoperiod sensitive, and 'Redkloud' and 'Redkote' were compared in a growth chamber with an LD of 16 h. More early than late progenies were included in the limited space of the growth chamber because the F_1, F_2, and F_3 data (see results) had suggested: (1) that photoperiod insensitivity was dominant in the growth chamber and was therefore more likely to continue to segregate and (2) that the variation of DTFF and nodal position of the first flower might result from control by several genes. There were four replications (a single plant in a pot) for each progeny and parent.

These F_8 plants were used as follows to determine whether photoperiod gene activity did or did not control partitioning. At 27 days after the first flower on each plant, the insensitive genotype was approaching maturity. For this reason, all aerial organs on each plant of both the insensitive and sensitive genotype were harvested on the 27th day after a first flower on that plant. Leaves, stems, and pods were separately dried for 6 or more days at 30 °C. The seeds were then separated from the pod walls, and all organs were weighed.

F_8 experiment 5. Partitioning in the field under LD

'Redkloud' and 'Redkote' plus 10 photoperiod-insensitive and 20 photoperiod-sensitive F_8 progenies, as classified in the LD greenhouse (Exp. 1), were compared in an Ithaca field planted June 16, 1987. More progenies of sensitive than insensitive genotypes were planted because, by now, greenhouse and growth chamber data from the homozygous F_8 progenies had established that the sensitive genotype is inherently more variable than the insensitive genotype for both DTFF and nodal position of the first flower. Three plots were planted for each progeny. Each plot was a row with five seeds planted about 10 cm apart, with an extra 10 cm between plots. Rows were 92 cm apart. DTFF was recorded for each plant. After observing that early or late flowering in the LD of the field always corresponded with the insensitive or sensitive genotype the F_8 progeny had expressed in the LD of the greenhouse and growth-chamber, we also recorded days to maturity, air-dry aerial biomass, and seed weight.

Experimental designs

A randomized complete block design was used in the greenhouse. Completely randomized designs were used in growth chamber and field.

Results

Bimodal segregation of 686 F_2 plants in the LD field of 1977, the ratio being about 27 early: 73 late (Fig. 1), suggested that control in that environment was by one gene. However, the bimodal early: late ratio had been nearer 33:67 for 150 F_2 plants in the field during 1976 (Fig. 1). This quantitative change between growing seasons of the apparent F_2 segregation ratio, plus reversal for both the F_1 and F_2 from genetic dominance for late flowering in the field to dominance for early flowering in the LD growth chamber (Fig. 1), cast doubt on the hypothesis of control by one gene. F_3 progenies can be grown only in an environment subsequent to and differing from that in which their F_2 parents were grown. The shift in the apparent F_2 segregation ratio by each environment invalidated F_3 progeny tests intended to verify previously observed F_2 segregation ratios (Masaya 1978). In addition to his hypothesis of control by one gene during the 1977 investigation, Masaya (1978) hypothesized likely control by a second gene, based on a model similar to the inheritance pattern hypothesized for photoperiod responses of sorghum (Quinby 1975) and peas (Murfet 1977). Masaya's model assumed that environmental differences altered epistatic interactions between two photoperiod genes.

The 1976 and 1977 field plantings were on June 9 and 10, respectively. The change in the apparent F_2 segregation ratio between years, therefore, was caused by environmental factor(s) other than daylength. The most likely cause was a difference in temperature between seasons. Differences in light quality (Mutters et al. 1989) may have caused the reversal of dominance between field and growth chamber (Fig. 1). A change in apparent segregation ratios by factors other than daylength has been reported by Padda and Munger (1969); Lenya et al. (1982); Gniffke (1982); compare Muhammad (1983) and Gniffke (1985).

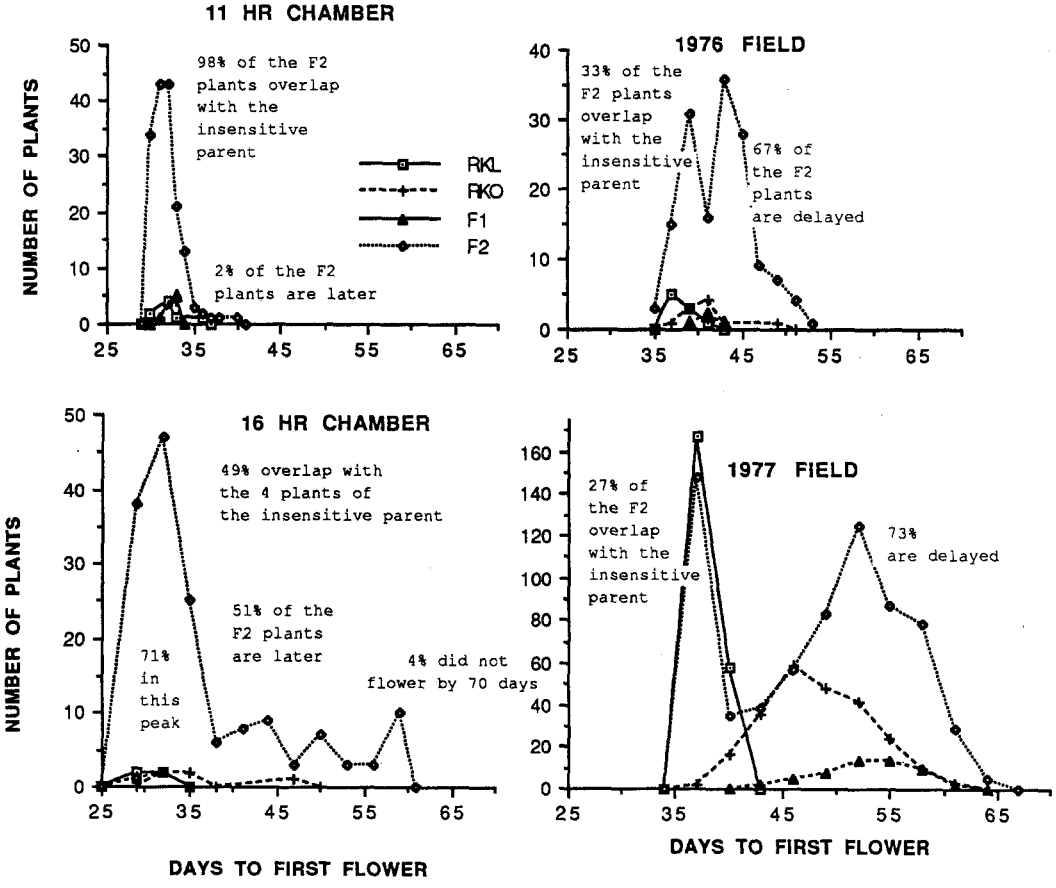

Fig. 1. Frequency distributions in four environments of the days to first flower for plants of the insensitive parent 'Redkloud', the photoperiod-sensitive parent 'Redkote', and their F_1 and F_2 generation progenies

F_8 experiment 1. Flowering phenotypes under long daylength

Of 89 F_8 progenies 43 had early DTFF with averages between 29 and 31 days. These progenies were photoperiod insensitive. The DTFF of all the individual plants (six siblings) within the 43 progenies was between 28 and 32 days, a span of but 5 days, which is the same span as for 'Redkloud', which averaged 30 days (Fig. 2).

The remaining 46 F_8 progenies had late DTFF with averages between 42 and 52 days. The average for 'Redkote' was 42 days. The DTFF of individual plants of the sensitive progenies spanned 31 to 58 days, a range of 4 weeks (Fig. 2). For only 15 of the 46 progenies did DTFF across the six sibling plants span as few as 5 days; for 13, DTFF spanned 6 to 10 days; for 18, the span was 11 to 25 days. The DTFF of the late parent 'Redkote' ranged from 31 days after planting, for just 1 plant, plus from 35 to 48 days for the remaining 23 plants, a total span of 18 days (Fig. 2).

For an individual plant early DTFF did not unambiguously indicate expression of photoperiod insensitivity. The single visually observable trait that unambiguously identified photoperiod insensitivity was a flush of flowers on the terminal inflorescence of the main stem on the day of or day after the first flower. A lack of this flush of flowers unambiguously

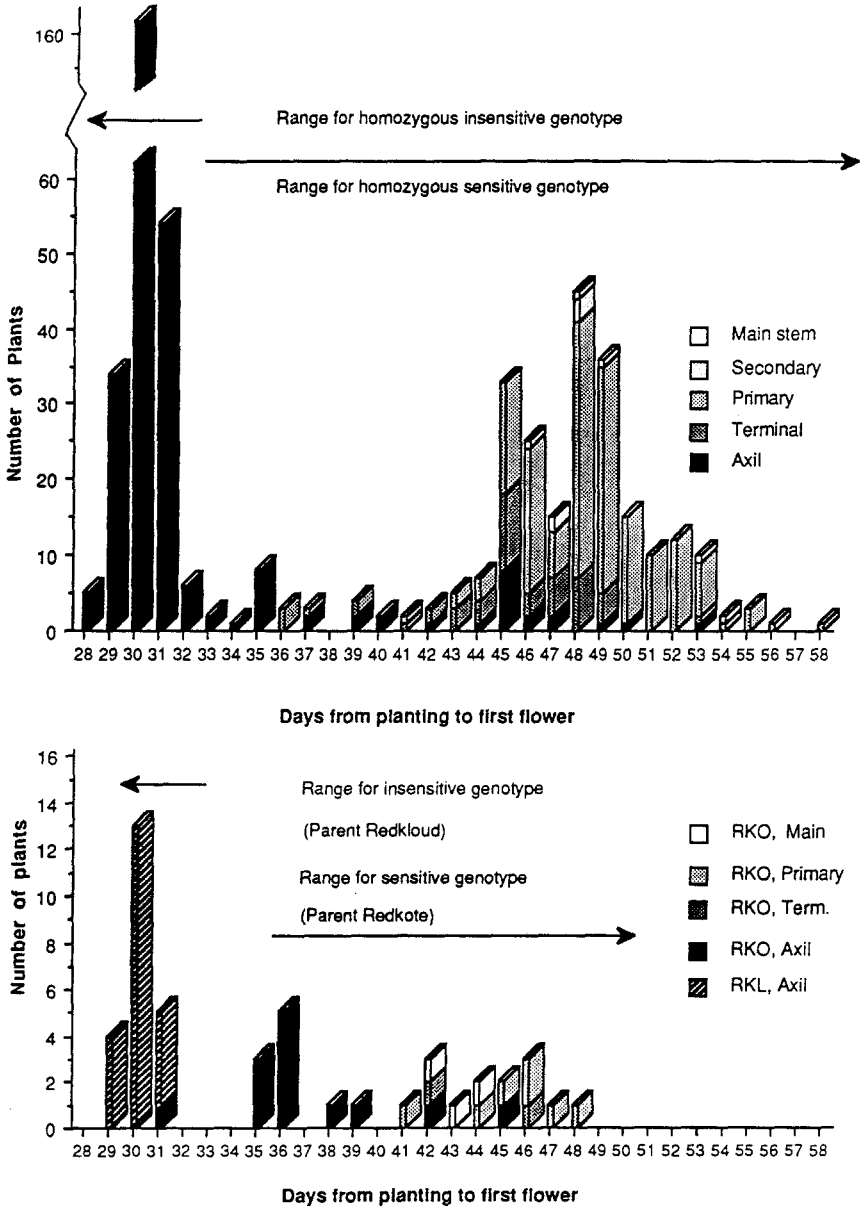

Fig. 2. Frequency distributions of both days to first flower and nodal position of the first flower for 534 plants from 89 F_8 generation progenies plus for 24 plants of the insensitive parent 'Redkloud' and 24 plants of the photoperiod-sensitive parent 'Redkote'

identified a plant as being of the photoperiod-sensitive genotype.

At DTFF of a plant of the photoperiod-insensitive genotype, there were always many large flower buds on the inflorescence that arises from the axil of the terminal leaf of the main stem, and these buds continued to grow rapidly. Most developed to anthesis within 1 day after DTFF, thereby providing the flush of flowers that identified the insensitive genotype.

Ten plants from nine homozygous photoperiod-sensitive F_8 progenies opened their first flower at the apex of the main stem and flowered distinctly earlier than their other siblings. One plant flowered on day 31; the others flowered on days 32–35, after the early parent 'Redkloud' but before all but 1 of 24 plants of the late 'Redkote' parent (Fig. 2). Each of the 10 plants had but one or two buds at the apex of the main stem. These bud(s) had grown slower than most of the larger number of buds on the insensitive genotype. A flush of flowers did not occur at this apex, verifying that these plants had the sensitive genotype like their siblings with larger DTFF.

Some siblings from 2 of the 46 F_8 progenies expressed photoperiod sensitivity, while others expressed insensitivity. These 2 progenies could represent the 1% expected to still be segregating for a gene, even after eight generations of selfing. This proportion could be enlarged by any outcrossing during insect visits to flowers. Accepting segregation within two F_8 progenies reduced the number of homozygous sensitive progenies to 44 compared with 43 insensitive progenies.

F_8 Experiments 2 and 3. SD versus LD reverse the flowering phenotype

The SD of the winter-time greenhouse (Exp. 2) reduced the mean DTFF of 17 sensitive progenies plus 'Redkote' to 32.8 ± 0.47 days from their 46.8 ± 2.54 days in the LD of the summer-time greenhouse (Exp. 1). The DTFF of the 17 insensitive progenies plus 'Redkloud' changed only from 30.0 ± 0.51 to 32.7 ± 0.35. Thus, under SD the sensitive and insensitive genotypes expressed the same early DTFF, the same low standard deviation of DTFF, and the same short span of DTFF among individual plants. Under SD, all of the plants of all 17 sensitive and 17 insensitive progenies developed many large buds, and every plant had the flush of flowers at the terminal inflorescence of the main stem that under LD had unambiguously indicated early flowering and the insensitive genotype. The change from late flowering under LD to early flowering under SD of the 'sensitive genotype' verified the expression of photoperiod gene activity.

The reduction in DTFF of the sensitive genotype in the greenhouse caused by SD as compared with LD also occurred in growth chambers (Exp. 3). LD caused a mean DTFF of 42.3 ± 9.20 for 2 sensitive F_8 progenies plus 'Redkote'; SD reduced this to 26.9 ± 1.02 days. Corresponding means for 'Redkloud' plus 2 insensitive F_8 progenies were 26.90 ± 0.46 days under SD and 27.5 ± 0.71 days under LD.

At DTFF under LD, the insensitive genotype had an average of 7.8 buds at the apex of the main stem in contrast to 2.5 smaller buds for the sensitive genotype. Under SD, the corresponding averages were 7.5 and 7.4 large buds.

F_8 experiment 4. Test of partitioning in a controlled LD environment

As in experiment 3, LD conditions in the growth chamber again resulted in fewer buds at the apex of the main stem of plants having the sensitive genotype than in those having the insensitive genotype. The respective averages were 2.0 and 8.4 buds, while DTFF averaged 39.0 and 29.0 days respectively. In addition,

Table 1. Pleiotropic effects on nine developmental traits by photoperiod-sensitive genotype *PPD* versus insensitive genotype *ppd* under 16-h daylength in the growth chamber

Output trait from the yield system	Photoperiod genotype		Least (99%) significant difference	Association with days to first flower
	Sensitive	Insensitive		
Days to first flower	39.0	29.0	2.4 days	
Bud number at apex of main stem	2.0	8.4	1.5 buds	Negative
Number of primary branches	8.9	7.9	1.2 branches	Positive
Number of nodes of (mostly secondary) branches	58.1	14.9	8.6 nodes	Positive
Aerial biomass	45.5	28.3	4.6 g	Positive
Biomass per day of plant growth	0.69	0.50	0.12 g	Positive
Seed weight at 27 days after first flower	0.85	11.3	2.69 g	Negative
Yield per day of plant growth	0.008	.201	0.30 g	Negative
Harvest index	2%	39%	4%	Negative
Seed number	3.0	33.0	7.3 seeds	Negative

the alternative genotypes caused differentials in number of nodes on branches, aerial biomass, biomass per day, yield per day, and harvest index (Table 1).

F_8 experiment 5. Test of partitioning in the field under LD

An average DTFF of 36 ± 3 for the insensitive genotype was attended by 88 ± 5 days to maturity, this contrasted with 48 ± 5 DTFF and about 120 days to maturity for the sensitive genotype. Maturity of the sensitive genotype was not accurately measured in the field because frost killed the latest plants. Average harvest index in the field from 58 F_8 plots of plants having the insensitive genotype was $0.50 \pm .07$ compared with $0.30 \pm .06$ for 114 plots of plants with the sensitive genotype. Harvest indices of 'Redkloud' and 'Redkote' were 0.50 and 0.40, respectively. These results verified that in the field each F_8 progeny expressed the same photoperiod insensitive or sensitive genotype it had already expressed in both the greenhouse and growth chamber.

Discussion

Days to flowering alone cannot differentiate photoperiod sensitivities

The most visually obvious trait that unambiguously differentiated the photoperiod-insensitive genotype from the photoperiod-sensitive one was the occurrence versus non-occurrence of a flush of flowers at the apex of the determinate main stem. Many flowers opened at this apex on the day of or day after a first flower on all plants of the insensitive genotype. Such a flush of flowers did not occur for any plant of the homozygous-sensitive genotype.

Time of initiation of flower buds could not be used to differentiate the insensitive and sensitive genotypes. Greenham (1982) showed for 'Redkloud' and 'Redkote' that their earliest initiation of flower buds occurs simultaneously under both SD and LD. Their first buds are initiated in the axil of the terminal leaf at the apex of the main stem, followed by initiation on the inflorescence that terminates this shoot. That photoperiod does not control time of bud initiation has also been shown for other bean cultivars (Morgan and Morgan 1984; Padda and Munger 1969; Gaytan and Kohashi-Shibata 1991). For this reason, beans have been classified as being photoperiod insensitive for floral bud initiation but photoperiod-sensitive for continued development of the flower buds (Salisbury and Ross 1991). The four independent studies all showed the delay in flowering of photoperiod-sensitive bean resulted because LD caused the buds to grow slower and/or to abort.

The response of bean to photoperiod is quantitative rather than qualitative. Inability to interpret inheritance of insensitivity versus sensitivity to photoperiod using the F_1, F_2, and F_3 generations resulted primarily from continuous variation of both days to first flower (DTFF) and the nodal position of that first flower. Quantitative variability resulted in a small difference in the ratio of early:late flowering between the LD field environments of two summers plus a much larger change of ratio by the LD of the growth chamber. Paradoxically, the genetic dominance for late flowering in the LD of the field was reversed to dominance for early flowering in the LD of the growth chamber. The interpretation of data for these early generations was limited additionally by not recognizing at that time that the differentiation of insensitive genotypes from sensitive ones is unambiguous only if based on the occurrence of a flush versus no flush of flowering at the apex of the main stem.

An additional constraint to interpretation of the F_1 and F_2 data was non-recognition at that time of differential variabilities for the genotypes with sensitivity and insensitivity to photoperiod. The homozygous F_8 progenies and parents demonstrated inherency of a short 3–4 day span of DTFF across all plants of the insensitive genotype in correlation with the appearance of 100% of the first flowers at the terminal node of the main stem. In contrast, a long 3–4 week span of DTFF was inherent to the sensitive genotype in correlation with the infrequent occurrence of the first flower at the terminal node of the main stem (observed for 18% of the plants with the sensitive genotype) and infrequent occurrence at the terminal node of a secondary branch (16% of the plants), but with most first flowers being at the terminal node of a primary branch (66%). DTFF tended to be later as the first flower shifted from the main stem to a primary branch to a secondary branch. 'Redkote' and 'Redkloud' and their F_8 progenies all have determinate shoots and, with few exceptions, the first flower is at the terminal node of the main shoot or of a branch.

Different variabilities of DTFF and the nodal position of that first flower in the insensitive and sensitive genotype are explainable by the hypothesis (Fig. 3) that photoperiod gene activity controls partitioning of the photosynthate between continuation of growth of the already initiated flower buds versus continuation of growth of additional leaves, nodes, and branches. Continued growth of the already (first) initiated reproductive (yield) organs will be enhanced as a larger proportion of the photosynthate is partitioned toward these organs. Any photosynthate partitioned toward continued vegetative growth will reduce the receipt of photosynthate by the flower buds, thereby slowing their growth and delaying their development to anthesis (extending the time to DTFF). Partitioning

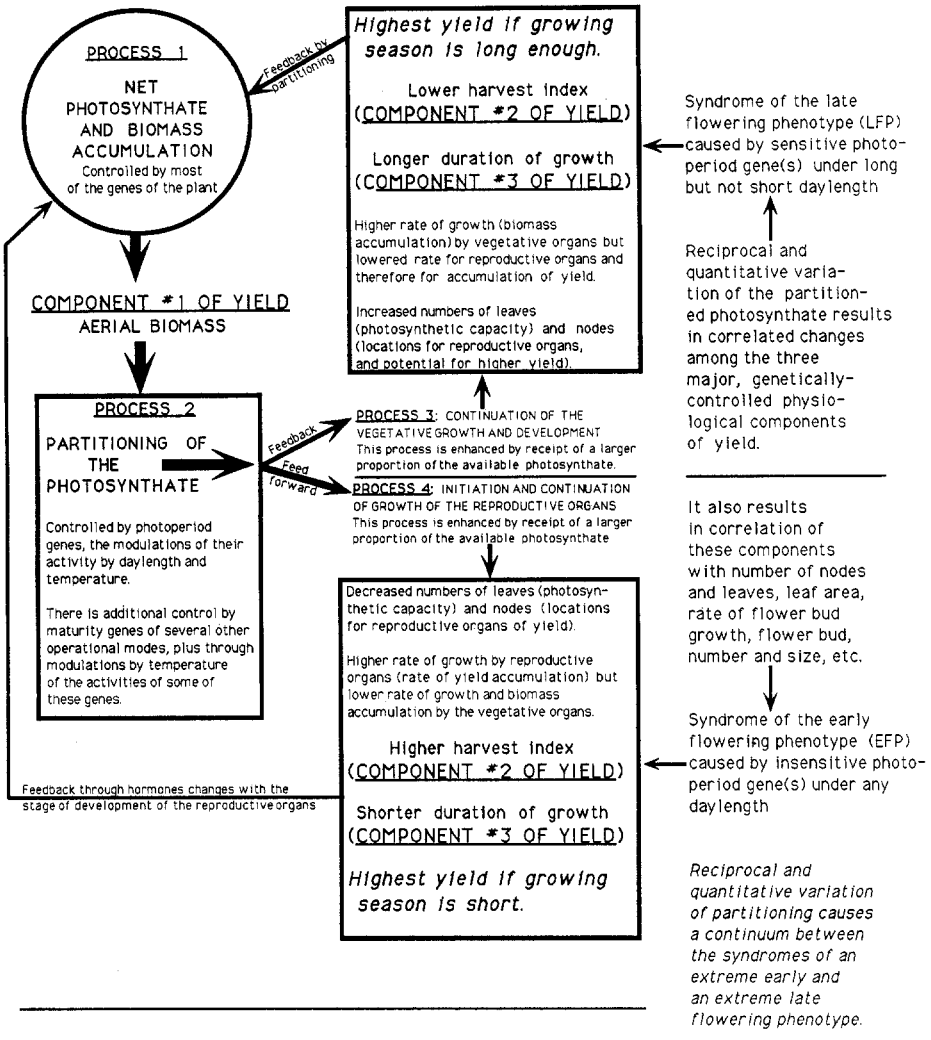

Fig. 3. Hypothesized role of photoperiod and other maturity genes in controlling partitioning and thereby controlling the harvest index, days to flowering and maturity, cultivar adaptation to growing season duration, and yield

a sufficiently large proportion to continued growth of additional vegetative organs can cause abortion of these first initiated buds, to delay DTFF even longer, by transferring the first flower from the terminal node of the single main stem to the terminal node of one of multiple primary branches. A delay in DTFF due to bud abortion will enlarge its variability because of the quantitative delay in DTFF that must attend transfer of the first flower from the single main stem to one of about ten branches. An additional delay of DTFF and nodal position by abortion of buds on primary branches and transfer of first flowers to secondary branches will further enlarge the variability. Consequent extension of exposure to additional variations of the environment will enlarge the variability further, as will any difference among the branches in competitive receipt of photosynthate (Fig. 3). Competitive access to the photosynthate will depend on the sequence of initiation of the branches plus on such differences as whether the branch is shaded by other leaves or can intercept the light needed for photosynthesis. Additionally, after any differentiation in development, the differentiated stage will respond differently to the same environment.

We interpret earlier than usual DTFF at the main stem on a few plants of the sensitive genotype to occur because as the other buds at this nodal position are aborted one or two remaining buds receive enough

photosynthate to develop relatively rapidly to anthesis. Several days follow before there are additional flowers, which are at later nodal positions (Masaya 1978).

Genotypes for insensitivity vs. sensitivity to photoperiod cause reciprocal levels of multiple traits

Segregation to give either photoperiod sensitivity or insensitivity of the F_8 generation in the LD environments of the growth chamber, greenhouse, and field in combination with the F_1 and F_2 segregations and other genetic data (Enriquez 1975; Masaya 1978; Gniffke 1982; Wallace et al. 1993b), plus comparisons from yield system analysis of yield trails (Bravo 1975; Kueneman 1978; Kueneman et al. 1979; Scully and Wallace 1990; Wallace et al. 1993a), have demonstrated the following. Under LD, the homozygous photoperiod-sensitive genotype always expresses not only later average days to flowering and absence of the flush of flowers at the apex of the main stem but also later days to maturity, larger aerial biomass, more branches, more leaves and nodes, larger total leaf area, lower rate of yield accumulation per day and lower harvest index. The levels of these 9 traits, plus the traits of larger variability discussed above of both the DTFF and nodal position of the first flower as well as the slower development of fewer and also smaller flower buds at the apex of the determinate main stem are a multiple-trait syndrome. This syndrome invariably attended the homozygous, photoperiod-sensitive genotype under LD (Fig. 3). SD interacted with this photoperiod-sensitive genotype to result in earlier flowering, earlier maturity, higher rate of yield accumulation per day, lower aerial biomass, fewer leaves and less leaf area, fewer branches, higher harvest index, less variability of DTFF and nodal position of the first flower, more and larger flower buds at the apex of the main stem, etc. The latter levels of the multiple traits are the syndrome expressed by the insensitive genotype under both SD and LD, and all levels of all traits of this early syndrome are the reciprocal (earlier or later, shorter or longer, larger or smaller, more or fewer, etc) of the levels of each trait as expressed by the sensitive genotype under LD. The reciprocal levels of all traits of the syndromes are inherited intact and in correlation with the genotype for sensitivity or insensitivity to photoperiod. Relationships to the three major genetically controlled components of yield (aerial biomass,

Table 2. A listing of traits with levels pleiotropically controlled by the interaction of the photoperiod gene *PPD* with long versus short daylength

No.	Trait with differential levels	Function or closest relationships to the three major component(s) of yield
1	Sensitivity to photoperiod	*Genetic control of all the traits*
2	Days to flowering	Related to days to maturity
3	*Days to Maturity*	*Major component of yield accumulation #3*
4	*Aerial Biomass*	*Major component of yield accumulation #1*
5	Number of branches	Related to aerial biomass
6	Number of nodes on shoots	Related to aerial biomass
7	Number of leaves	Related to aerial biomass
8	Leaf area	Related to aerial biomass
9	Rate of yield accumulation per day of seedfill	*Causal of harvest index and days to maturity* (viewed from a physiological perspective)
10	Rate of yield accumulation per day of growth	*Causal of harvest index and days to maturity* (viewed from an economic perspective)
11	*Harvest Index*	*Major component of yield accumulation #2*
12	Variability of days to flower	Related to gene effect on nodal position
13	Variability of nodal position	Related to gene effect on nodal position
14	Flush of flowers	Related to harvest index and days to maturity
15	Number of buds at apex of main stem	Related to harvest index and days to maturity
16	Size of buds at apex of main stem	Related to harvest index and days to maturity
17	Preflowering partitioning rate	*Causal of days to flowering*
18	Postflowering partitioning rate	*Causal of harvest index and days to maturity*
19	Rate of biomass accumulation	Related to aerial biomass
20	Rate of vegetative development	Related to aerial biomass and days to maturity
21	Seedfill duration	Related to harvest index and days to maturity
22	Rate of development to flowering	= 1/days to flowering
23	Rate of development to maturity	= 1/harvest index and days to maturity
24	Node of the first flower	Morphological equivalent of the days to flowering
25	Sink strengths of reproductive versus vegative organs	*Physiological cause of the variable and alternative levels of all the traits*
26	Yield	The economic output of the system

harvest index and days to maturity) plus levels of 22 additional traits of the early and late syndromes are summarized in Table 2. All 22 traits are simply alternative perspectives relative to one or two of the three major genetically controlled components of yield, but the relationships do not always become obvious until all 25 traits are viewed either as partitioning per se, as a control over the partitioning, or as a consequence of the partitioning of photosynthate between reproductive and vegetative growth.

F_8 verification of one photoperiod gene

The 43 homozygous F_8 progenies which inherited early flowering in any daylength in comparison to the 44 which inherited late flowering in LD but flowered early in SD is as close as possible to the bimodal 1:1 segregation ratio expected from control by one photoperiod gene. This allows acceptance of the hypothesis of control by one photoperiod gene suggested by the 27:73 (1:3) F_2 ratio in the field in 1977 (Fig. 1). The reversed F_2 segregation ratio 71:29 (3:1) in the LD growth chamber, i.e., reversal of dominance for late flowering in the field to dominance for early flowering in the LD chamber, became interpretable as being bimodal and control by the same single photoperiod gene after demonstration by the F_8 progenies that the homozygous-sensitive genotype inherently causes a larger span of DTFF and a more variable nodal position of first flower than the insensitive genotype. Reversal of dominance with maintenance of an F_2 ratio for one gene would result if the LD environment of the growth chamber delayed DTFF of the homozygous genotype but failed to delay DTFF of the heterozygous genotype, which has a single sensitive allele. The intermediate 33 early:67 late in the field in 1976 can be explained, similarly, as failure of that environment to fully delay flowering of every heterozygote. In support of such a quantitatively variable delay of the heterozygotes due to environmental influence, the DTFF of F_2 plants giving the late peak of flowering of the 1976 field was delayed to a maximum of 53 days after planting compared with 67 days in 1977 (Fig. 3), and the respective averages were 45.0 and 52.2 days (Table 3).

Activities of the two alleles of the photoperiod gene

The F_8 data indicate that in its homozygous state the insensitive allele allows constitutive development to flowering under both SD and LD. Inactivity of the photoperiod-sensitive allele under SD also allows this inherent development to flowering, but LD activates the sensitive allele, which then delays flowering. We label the insensitive allele *ppd* and the sensitive allele *PPD*. The small versus capital letters indicate the genetic dominance versus recessiveness observed in the field (Fig. 1, Table 3; Masaya 1978).

The *ppd* and *PPD* alleles may correspond, respectively, with alleles of bean designated as *neu* (neutral) and *Neu* (photoperiod sensitive) by Rudorf (1958). We use *PPD* because *ppd* is not neutral; it causes a slight delay of DTFF under high temperature combined with LD (Muhammad 1983; compare White and Laing 1989). *PPD* and *ppd* almost certainly correspond with one of two photoperiod genes that Padda and Munger (1969) symbolized as *Ht* and *Lt*. Gene *Ht* delayed flowering in LD only in combination with high temperature (25 °C); *Lt* delayed flowering only at a low temperature (15 °C).

The syndromes result from pleiotrophic effects by the photoperiod gene

Rieger (1976) described pleiotrophy as: 'The production by one particular mutant gene of apparently unrelated multiple (or manifold) effects at the phenotypic level'. Rieger stated that pleiotrophy reflects the integrated state of cellular and developmental metabolism and causes a 'genetic syndrome'. Our interpretation is that the reciprocal levels of the multiple traits that constitute the syndromes of the photoperiod-sensitive and insensitive genotypes are all due to control by the photoperiod gene over the partitioning.

Table 3. Mean days to first flower of an insensitive parent ('Redkloud'), a photoperiod-sensitive parent ('Redkote') and their F_1 and F_2 generation progenies

Environment	Mean days to first flower[a]			F_2	
	Redkloud (insensitive)	Redkote (sensitive)	F_1	Early	Late
11 h growth chamber	30.6	32.6	32.7	31.8	39.3
16 h growth chamber	30.5	33.5	31.0	30.7	43.7
Field in 1976 (16 h)	39.1	40.1	41.0	38.9	45.0
Field in 1977 (16 h)	36.3	48.3	51.7	38.0	52.2

[a] The means are the average of the parental and bimodal F_2 distributions shown in Fig. 2

Pleiotrophy results from competition for photosynthate

Pleiotrophic expressions of the levels of all 25 traits of the syndromes that attend the insensitive and sensitive genotypes under LD (Table 2) are fully explainable if the alternative alleles of the photoperiod gene cause alternative levels of partitioning of the available photosynthate between continuation of growth and development of the first initiated reproductive (yield) organs versus continued growth and development of more branches, nodes, and leaves (vegetative organs) (compare Fig. 3). The same molecule cannot simultaneously support growth and development of both reproductive organs and additional vegetative organs.

The hypothesized competitive partitioning of reciprocal levels of photosynthate toward the continued reproductive growth and development versus continued vegetative growth and development (Fig. 3) suggests that increases or decreases in the time used to develop to maturity will be changed complementarily by the reciprocally received quantities of photosynthate. Complementarity is illustrated as follows. Partitioning more of the photosynthate to the continuation of vegetative growth will enlarge the numbers of nodes and leaves on the plant, plus the number of later-initiated reproductive (yield) organs (Fig. 3). The larger leaf area (increased capacity for photosynthesis) will reinforce enhancement of the continued vegetative growth. Consequent extension of the time used to develop to flowering and maturity will be reinforced by a lowered rate of growth (or even abortion as reported above) of the already initiated reproductive organs (Fig. 3).

Alternatively, partitioning the larger proportion of the photosynthate to the growth of already existing buds and the resulting flowers, pods, and seeds will accelerate their rates of growth. The shorter time the reproductive organs will need to develop to flowering and harvest maturity will be reinforced by a reduction in the rates of vegetative growth and development that arises from the reduced proportion (quantity) of the photosynthate that these vegetative organs receive (Fig. 3). Additional reinforcement will arise as the reproductive organs approach maturity. At this stage, the reproductive organs will provide altered hormonal signals that will hasten senescence of the whole plant.

Photoperiod gene control over sink activity

Sink activity (rate of assimilate uptake per unit weight of sink tissue) multiplied by sink size (organ weight) equals sink strength, as defined by Wareing and Patrick (1975). The bean data presented suggest that a (presumed but untested) change of hormonal balance (Fig. 3) caused by activity of the photoperiod-sensitive allele reduced the constitutive sink activity of the reproductive organs under a non-promotive daylength (LD). Statistically equal numbers of buds at this nodal position under SD plus equal bud size, for both the insensitive and sensitive genotype, suggest that the simultaneous initiations of earliest flower buds at the terminal apex of the main stem of the two genotypes began with equal sink size (biomass of the cells that develop into reproductive organs). A subsequent 75% reduction by the sensitive genotype when functioning under LD of the number of buds, plus an accompanying reduction of their size, suggests that the sensitive genotype negatively controlled the sink activity of the reproductive organs under LD, whereas under SD this sink activity remained constitutive like that of the insensitive genotype. Reduction of sink activity occurred at both the post-initiation and post-flowering stages of the reproductive development and was reciprocally compensated by an increase in the sink activity of the vegetative organs, which resulted in additional branches, leaves, and nodes.

Photoperiod gene control over yield

The three major physiological componenets of yield (aerial biomass, harvest index, and days to maturity) were all pleiotropically altered in level by photoperiod gene activity (compare Wallace et al. 1993b). We suggest that the ability to breed for cultivar maturity, adaption, and higher yield can be enhanced (Wallace et al. 1993a) by elucidating the activities of different photoperiod genes and alleles, by quantifying the modulations of these gene activities by daylength and temperature, and by quantifying the interactions between photoperiod genes and other classes of maturity genes.

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