

## A whole-system reconsideration of paradigms about photoperiod and temperature control of crop yield

D. H. Wallace<sup>1</sup>, R. W. Zobel<sup>2</sup>, and K. S. Yourstone<sup>3</sup>

<sup>1</sup> Department of Plant Breeding and Biometry, Cornell University, Ithaca, N.Y. 14853, USA

<sup>2</sup> USDA-ARS, Department of Soil, Crop and Atmospheric Sciences, Cornell University, Ithaca, N.Y., USA

<sup>3</sup> Department of Fruit and Vegetable Sciences, Cornell University, Ithaca, N.Y., USA

Received September 4, 1991; Accepted May 7, 1992  
Communicated by A. R. Hallauer

**Summary.** Effects by photoperiod gene(s) and day-length on crop yield and its three major physiological components (aerial biomass, harvest index, and days to harvest maturity) are reviewed for bean (*Phaseolus vulgaris* L.) and peanut (*Arachis hypogaea* L.). In these plus many other cited crops, photoperiod sensitive gene(s) delay days to flowering and/or days to maturity in non-promotive daylength while simultaneously lowering the harvest index. Thus, for many crops, earlier maturity is associated with higher harvest index, and/or it has been shown that photoperiod gene(s) control partitioning of photosynthate toward reproductive growth versus toward competitive partitioning to continued vegetative growth. Our conclusion is that photoperiod gene control over this partitioning precedes and is causal of the photoperiod-gene control over days to flowering and maturity. This implies shifts from commonly accepted paradigms about effects by photoperiod and about breeding for higher yield. These paradigm shifts suggest more efficient ways to breed for cultivar adaptation to the specific growing season duration and environment of each geographical site and for higher crop yield.

**Key words:** Yield physiology – Phenology – Crop adaptation – Harvest index – Crop maturity – Aerial biomass

### Introduction

The paradigm that the concentration of one or more hormones controls plant development has failed to

explain most developmental variabilities of plants (Trewavas 1986; Guern 1987). Trewavas (1986) stated: 'In biology we deal with the most complex systems known. ...Complex situations are surely going to require complex explanations if the explanation is to be accurate. Or if we retain simple views should we not honestly admit that they may achieve little when faced with biological complexity'. Trewavas's statement was cited in a review of photoperiodism and morphogenesis (Bernier 1988). Trewavas additionally stated: 'Biological systems include a great density of connections between parts of the system'. He recommended research at the whole-system level of plants. These complexities are compounded by difficulty in documenting and/or measuring the interactions among the parts of the system (Zobel 1990, 1992).

Trewavas (1986) recognized that the notion of scientific advance through the refutation of hypotheses originated in biochemistry and physics for which reductive simplicity enables 'all or none' experimental approaches. He doubted the 'all or none' confirmation or rejection of hypotheses based on whole biological systems because the number of variables is almost infinitely large and suggested that conclusions can be relative but not definitive, that acceptance of biological hypotheses can only be conditional.

This review suggests and describes the need for multiple shifts from current paradigms on the physiological genetics of yield. All of the shifts were suggested by results from studies of the yield system of bean, with backup from similar results found in peanut and other crops. The initial research with bean began with the hypothesis that capacity for photosynthesis (leaf area – Wallace and Munger 1965, 1966) and/or rate of leaf photosynthesis (Izhar and Wallace 1967) could assist in breeding for higher yield. At that time technologically

advanced tools easily identified statistically significant genetic differences in photosynthetic rates. Unfortunately, a change of environments reversed levels among the genotypes, and inheritance involved so many genes that even with a controlled environment, heritability was so low that selection among segregates was ineffective. Levels of photosynthetic traits do not correlate with yield (Wallace et al. 1972, 1976; Wallace 1980; Wallace and Zobel 1982; compare Gifford 1986, 1987).

Since photosynthetic traits did not assist in breeding for higher yield, the research shifted (Wallace 1973; Wallace and Masaya 1988; Wallace et al. 1993a) toward measurement of yield's major, genetically controlled physiological components: biomass, harvest index, and days to maturity (Fig. 1). Jointly, levels of these three major components fully account for the yield. The levels of all three are usually correlated with yield when compared across all tested genotypes within each yield trial (Wallace et al. 1993a). Compared across many yield trials, biomass and harvest index are almost always positively correlated with yield. On the contrary, days to harvest maturity may be as often negatively correlated as positively. Yields

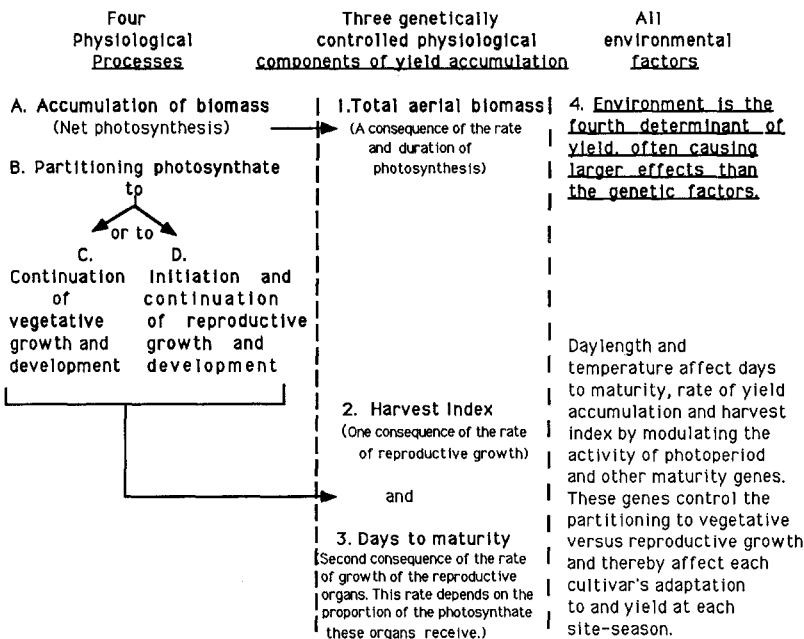
which arise from different combinations of its major physiological components represent alternative integrations of the thousands of gene actions that collectively result in yield accumulation. Comparisons of the same genotype(s) across planting dates, years, or geographical sites quantify the variations in its major physiological components and in yield caused by environmental influences on the integrated gene activities.

The time a cultivar uses (needs) to develop to harvest maturity becomes the third genetically controlled component because: (a) biomass is accumulated at an average rate across this time; (b) yield per se is accumulated as a proportion of this net photosynthate is partitioned toward the yield (seeds, tubers, or bulbs, etc.) at an average rate across a finite duration of seedfill, or enlargement of tubers, bulbs, etc.

*Evidence for photoperiod control over partitioning*

A cross was made with the expectation of raising yield by genetically recombining the high aerial biomass of one bean cultivar with the high harvest index of a second (Wallace et al. 1993a, b). The progeny expressed genetic linkages among the physiological components

The major components of the yield system of crop plants consist of:



Reciprocal sharing of photosynthate results in reciprocal changes of rates of processes C and D. Reciprocal rates of C and D alter the rate of growth of the reproductive (yield) organs, thereby changing the duration of growth (the days to maturity which is the genetically controlled yield component #3 and simultaneously altering the harvest index (yield component #2). These physiological-genetics of the yield system explain why yield advances have been predominantly through higher harvest index with little improvement of biomass. They suggest a strategy of breeding that can also raise the biomass. (Adapted from Fig. 3 and Table 2 of Wallace et al 1993b; compare also Fig. 1 of Wallace et al. 1993a).

**Fig. 1.** Four major genetically controlled processes and three physiological components of yield accumulation and their interrelationships

of yield, and the linkages were correlated with segregation of a single photoperiod gene (Wallace et al. 1993a, b). Compared against the photoperiod-sensitive allele of the photoperiod gene, the insensitive allele caused earlier flowering, earlier maturity, a higher rate of yield accumulation, and higher harvest index, but reduced both leaf area and biomass accumulation (Wallace et al. 1993b). It is recognized that yield and its components can all be altered by both the genotype and environment, as well as by the genotype  $\times$  environment interaction (Crossa 1990). Environment is not genetically controlled, but it is the fourth major determinant of the yield (Fig. 1; Fig. 1 of Wallace et al. 1993a, Fig. 3 of Wallace et al. 1993b).

Control by a single photoperiod gene over at least 25 traits related to yield, a few having just been specified in the previous paragraph and all in Wallace et al. (1993b), illustrates the 'great density of connections between parts of the system' referred to by Trewavas (1986). The shifts from accepted paradigms suggested hereafter all arise from an improved understanding of the interconnections (Fig. 1) among the three major, genetically controlled physiological components of yield, including modulations of the levels of these components and the interconnections among them by daylength and temperature (Wallace et al. 1991, Wallace et al. 1993a, b).

We have experienced difficulty in comprehending, describing, and explaining in simple terms the inherent complexity of the *serial controls and interacting feedback and feedforward consequences* represented by interconnections among the four determinants of yield: biomass, harvest index; days to maturity, and the total environment. These interactions are partially described above and are considered further below (compare Fig. 1 and Figs. 1 and 3 of Wallace et al. 1993a, b, respectively). A reader's initial comprehension of our descriptions (Wallace et al. 1991, 1993a, b), including this review, will be constrained by the complexities of the system, and more so by the shifts from commonly accepted paradigms. As Trewavas (1986) suggested, initial comprehension and acceptance will be interpreted in accordance with the reader's attitudes as engendered by training, background, and personality. Initial attitudes will incorporate the commonly accepted paradigms derived from reductive research, rather than the shifts of paradigm described hereafter, which are derived from whole-system research.

#### *Paradigms relative to partitioning and yield*

This review considers eight paradigms accepted by most plant scientists; all relate to the yield system of crop plants. Each paradigm is presented, followed by one or more suggested shift(s) from that paradigm,

and by bases for the shifts. Each shift is derived from the effects of photoperiod on yield and its physiological components as reviewed herein for both bean and peanut. Both of these crops flower and/or mature quantitatively earlier in response to shorter daylength. Similar effects by photoperiod and/or maturity genes are cited for 22 additional crops, including species that flower quantitatively earlier in response to longer rather than shorter daylength.

#### *Paradigm 1. Photoperiod directly controls the time of initiation of flower buds and thereby controls the time of flowering*

Paradigm 1 has become accepted because of the focus by basic research on control by daylength over the initiation of flower buds. The species studied were selected because they have such an extreme sensitivity to daylength that as little as one short or long day changes development from continued vegetative growth to reproductive growth. Species with this *qualitative* response are preferred for basic research because they give the uniformity of response needed for hormonal and molecular assays. The average plant scientist accepts paradigm 1 because the extensive literature on photoperiodism deals almost entirely with completed basic research aimed toward elucidation of molecular phenomena.

In light of the effects by photoperiod on yield and its physiological components, paradigm 1 must be shifted to the following four more general concepts: (1) *Depending on genotype and environment, photoperiod may control any or all stages of reproductive development (yield accumulation).* (2) *The direct effect by photoperiod gene activity is control over the partitioning of photosynthate.* (3) *Photoperiod control over the partitioning is causal of its control over the times to bud initiation, flowering, and maturity.* (4) *Dependent on genotype and environment, photoperiod can also control the partitioning to storage organs such as tubers, bulbs, and roots (yield) of certain crops.*

Justification: many crop plant species will flower in any daylength and show quantitative (rather than qualitative) control by daylength over days to flower. Although limited to one or a few paragraphs in books or chapters within books, Vince-Prue (1975, 1982, 1983) and Salisbury (1963) clearly state that, depending on the species, daylength may control any stage in the development of reproductive organs. Salisbury (1963) and Salisbury and Ross (1991) emphasize extensive differences among species (and/or genotypes) for the stage of reproductive development modulated by daylength. The first and fourth shifts from paradigm 1 have been accepted by other scientists involved in photoperiod research, but are also discussed in just a few sentences or paragraphs in their reviews of photo-

periodism (Kinet et al. 1985; Bernier 1988; Beverage et al. 1992; Hodges 1991). The average plant scientist acquires and adheres to paradigm 1, even after reading Vince-Prue's and Salisbury's books, or reviews of photoperiodism by others, because most of the literature on photoperiodism focuses on time to initiation of flower buds. The paucity of research on control over other stages of reproductive development has resulted in the failure to assess their biological importance.

Four recent, independent studies report that photoperiod does not control time of flower bud initiation in bean. Instead, the stages controlled are rate of continued flower bud growth and development (Greenham 1982; Morgan and Morgan 1984; Padda and Munger 1969; Gaytan and Kohashi-Shibata 1991) plus the continued rate of growth and development of the pods and seeds (Wallace et al. 1993b). In peanut, response to photoperiod occurs at a yet later stage of development; with no control over either flower bud initiation or time to flowering, long daylength extends the duration of the pod-filling phase, lowers the harvest index, and increases the rate of biomass accumulation, while decreasing yield (Witzenberger and Lenz 1988; Flohr et al. 1990; Bagnall and King 1991; Bell and March 1991). Partitioning to reproductive sinks of peanut cultivars was greater (harvest index was higher) under natural short daylength in tropical fields than under incandescent lamp-extended daylength. The shorter daylength simultaneously reduced the aerial biomass. Coffelt et al. (1989) observed that early maturing peanut cultivars have higher harvest indices than late cultivars. Witzenberger and Lenz (1988), Flohr et al. (1990), and Bagnall and King (1991) review other studies (mostly in growth chambers) of photoperiod response in peanut. Both growth chamber and field studies show reciprocal (competitive) changes between reproductive versus vegetative growth.

#### *Mechanistic bases for shift from paradigm 1*

It was found for bean that a single photoperiod gene can control the proportion of the photosynthate partitioned toward continued growth of the earliest initiated flower buds (Wallace et al. 1993b). The first buds on both the insensitive and photoperiod-sensitive genotype are initiated at the same nodal position and number of days after planting (Greenham 1982). Two alternative and competing scenarios may occur after bud initiation. Alternative 1 is preferential partitioning of the photosynthate to continued growth of additional stems, branches, and leaves. This occurs for the photoperiod sensitive genotype in long daylength (Fig. 3; Wallace et al. 1993b). Because the already initiated flower buds receive reduced photosynthate, they grow slowly, develop slowly, and need more days before

flowering (anthesis), i.e., the rate of development (1/days) to flowering) will be low. If the buds receive still less photosynthate, they abort. Subsequently, flowering will not occur until buds initiated at later nodes have grown and developed to anthesis. Alternative 2 is preferential partitioning of the photosynthate to existing flower buds with compensatory reduction of partitioning to continued growth of additional nodes, leaves, and shoots (Fig. 1). This occurs for the photoperiod-insensitive genotype under both short and long daylength and for the sensitive genotype under short but not long daylength. When the flower buds receive a larger proportion of the photosynthate they grow rapidly, and a larger number of larger sized buds develop to flowering in a shorter time (Wallace et al. 1993b). The rate of development to flowering (1/days) is high:

Continuation after flowering of preferential growth of pods and seeds (rapid reproductive growth) compensatorily decreased (Fig. 1) the continuation of growth of more stems, branches, and leaves (vegetative growth) Wallace et al. 1993b). Compared with the sensitive genotype, under long daylength the photoperiod-insensitive genotype flowers earliest, develops to harvest maturity earliest, accrues a higher harvest index, and has both a higher rate of yield accumulation per day and a compensatory lower rate of accumulation of leaf area and total aerial biomass (Fig. 1; Fig. 1 of Wallace et al. 1993a; Fig. 3 of Wallace et al. 1993b). Development of the sensitive genotype was changed by short daylength to duplicate that of the insensitive genotype under any daylength.

#### *Paradigm 2. Competition occurs between yield accumulation and continued vegetative growth*

The above discussion of bases for modifying paradigm 1 implies the following modification of paradigm 2. *Depending on species and environment, competition between reproductive growth (yield accumulation) and concurrent vegetative growth can occur at any and/or all stage(s) of reproductive development.*

Yield physiologists expect reduced yield if photosynthate is partitioned toward continued vegetative growth rather than toward the organs of yield (Lawn 1989; Squire 1990; Lambers et al. 1990). The shift from paradigm 2 suggested is merely that: competition between reproductive and vegetative organs for photosynthate can, depending on the species or genotype, occur at least as early as immediately after (Wallace et al. 1993a, b) and even prior to flower bud initiation (Beverage et al. 1992). Beverage et al. (1992) found for sweet pea that partitioning of photosynthate was altered prior to bud initiation by the genotype with sensitivity to photoperiod. This change in

partitioning was not a consequence of initiation as commonly assumed but preceded it (Flohr et al. 1990; Richards 1991). The shift from paradigm 2 is simply an application at earlier developmental stages than yield physiologists usually consider. For bean this earlier application is indicated by an association of the genotype for photoperiod insensitivity with more rapid flower bud growth than the insensitive genotype. This is followed by earlier flowering and earlier maturity plus higher harvest index, all in combination with a higher rate of yield accumulation but a lower rate of biomass accumulation (Fig. 1) (Wallace et al. 1993a, b). In support of the shift from paradigm 2, the photoperiod-sensitive bean genotype expresses the just described relative levels of all these traits if grown under short rather than long daylength. Short daylength prevents activity by the sensitive photoperiod gene.

The shift from paradigm 2 is also supported by the effects of photoperiod on the physiological components of yield of peanut. Short daylength causes higher harvest index combined with earlier maturity and higher rate of accumulation of yield, but lowers the rate of biomass accumulation (Witzenberger and Lenz 1988; Flohr et al. 1990; Bell and March 1991).

The shifts of both paradigms 1 and 2 are based on evidence in both bean and peanut that photoperiod gene activity controls the partitioning of the photosynthate to reproductive organs versus to vegetative organs. In bean the partitioning controls the rate of post-initiation continuation of reproductive growth (rate of biomass accumulation by buds, pods, and seeds; i.e., the rate of yield accumulation) versus the rate of accrual of more nodes, leaves, and total biomass (rate of continuation of vegetative growth) (Fig. 1; Fig. 1 of Wallace et al. 1993a; Fig. 3 of Wallace et al. 1993b). It is commonly believed (Nooden 1987) that seeds exert the principal control over the rate (1/days) of development to plant maturity. We propose that one basis for predominant control through the reproductive organs is the larger the proportion of the photosynthate partitioned to them the faster the reproductive organs will grow (i.e., the higher the rate of accumulation of biomass as yield) and the fewer the days they will need to develop to harvest maturity. As the slow or rapidly developing seeds approach maturity a second basis for differential maturity occurs: hormonal signals that emanate from the seeds change to stimulate senescence and maturity of the whole plant (Fig. 3 of Wallace et al. 1993b).

In peanut, Flohr et al. (1990) concluded that fruit initiation and developmental change were reflected by subsequent partitioning of assimilates to the pods. This is the inverse of our reasoning that gives rise to paradigms 1 and 2. We reason that developmental rates and durations are a consequence of the proportion of

the photosynthate partitioned to the reproductive organs and of the consequent rate of growth of these organs. Flohr et al.'s reasoning (1990) and that of Richards (1991) differs from ours only as to which is the biological cause and which is the effect: partitioning versus the time to develop to the specified stage. Flohr et al. (1990) considered our reasoning (Wallace et al. 1993b) that partitioning is causal, by suggesting the possibility that long daylength caused the shoots to become a stronger sink than the reproductive organs. They decided this was unlikely because the fruits had already been initiated; i.e., by assumption that time (of initiation) is causal. Evidence in sweet pea that photoperiod gene control over partitioning precedes flower bud initiation (Beverage et al. 1992) supports our reasoning that partitioning is causal. Beverage et al. (1992) suggest that control over partitioning prior to flower bud initiation supports the nutrient diversion hypothesis of Sachs (1987). Compared with our hypothesized causal effect by control through photoperiod gene control over partitioning, the nutrient diversion hypothesis differs only in that it was described only in reference to control over flower bud initiation; relationships between partitioning and yield were not considered.

*Paradigm 3. The days to maturity of a cultivar establishes its adaptation to the duration of the growing season at each site and thereby strongly controls yield of the cultivar*

Paradigm 3 needs the following modification. *The rate of reproductive growth (rate of yield accumulation), plus the rate of growth prior to flowering (Damisch and Wiberg 1991), of a cultivar establish the adaptation of each cultivar to the duration of the growing season of each site-season and thereby strongly control the yield.*

*Basis for the shift in paradigm 3*

The shifts from paradigms 1 and 2 suggest an apparent paradox relative to paradigm 3. It is: the rate of yield accumulation (the proportion of the photosynthate partitioned to the reproductive organs) controls the days to maturity, thereby controlling the adaptation of the cultivar to the duration of the growing season and subsequently, the effects by this adaptation on the yield. The ostensible contradictions are not contradictions, since the time any plant organ requires to develop to a specific stage is a consequence of its rate of growth (Summerfield and Roberts 1988, 1990). What is illustrated is that feedback and feedforward effects within the yield system are *interconnected* (compare Fig. 1 with Fig. 3 of Wallace et al. 1993b).

*Paradigm 4. Days of flowering and to maturity are genetically independent of the harvest index (of partitioning)*

This paradigm is commonly applied toward breeding for higher yield. Paradigm 4 is invalid because the proposed shifts from paradigms 1 and 2 imply the following shift from paradigm 4: days to flowering and maturity are *interconnected* with the harvest index because maturity genes control the partitioning and its consequent control over both harvest index plus the days to flowering and maturity (Wallace et al. 1993b).

*Paradigm 5. Control over competition for photosynthate between continued vegetative growth versus continued reproductive growth is independent of the genetics for days to flowering and maturity*

The shifts from paradigms 1 and 2 also invalidate paradigm 5 which, like paradigm 4, is routinely applied to breeding for higher yield of many crops, although usually unstated. The control by photoperiod and other maturity genes (Wallace et al. 1993a,b) over the allocation of photosynthate to continuation of reproductive growth versus to continuation of growth and development of additional vegetative organs interconnects the genetics of partitioning with the genetics of days to flowering and maturity. Photoperiod gene activity is progressively enlarged as daylength is extended (for short-day plants) or shortened (for long-day plants). Photoperiod gene activity is also amplified synergistically if temperature rises simultaneous with the extension of daylength (Wallace et al. 1991, 1993a,b). The higher temperature will simultaneously enhance the rate of node development, delay the node to flower, and amplify other components of both vegetative and reproductive growth. Thus, multiple interconnections between reproductive and vegetative growth and development, in addition to common control by photoperiod gene activity, result in extensive interactions between vegetative and reproductive growth and development that partially control the time durations to flowering and maturity.

*Paradigm 6. Partitioning of photosynthate becomes important only after flowering*

Paradigm 6 is a common but usually unstated assumption. That it is invalid is indicated by our demonstration in bean (a short-day species) that long daylength alters the partitioning and subsequent development and yield as early as directly after flower bud initiation (Wallace et al. 1993b) and by the demonstration by Beverage et al. (1991) in sweet pea

(a long-day species) that short daylength alters the partitioning even prior to flower bud initiation (additional details are in the discussion of shifts from paradigm 2). The bean and even more so the sweet pea data imply that the earliest changes toward reproductive development involve competition for photosynthate between reproductive growth and development versus any continuation of initiation, growth, and development of additional nodes, leaves, and shoots (vegetative development).

*Paradigm 7. The appropriate daylength causes flowering*

The observation that an appropriately short or long daylength results in flowering of qualitatively responding plant species leads, often unconsciously, to acceptance of paradigm 7. Paradigm 7 is more correctly stated as: *The inappropriate daylength delays flowering*. The results reviewed above for bean indicate that the photoperiod-insensitive genotype has constituent development toward flowering. The sensitive genotype has the same inherent capability also, since it always initiates flower buds simultaneously with the insensitive genotype. Its flowering is delayed under long daylength by a lowered growth rate of the buds, but when under a short photoperiod that promotes flowering it expresses the same rate of bud growth as well as equivalent levels of at least 25 additional reproductive and vegetative traits as the insensitive genotype (Wallace et al. 1993b). This suggests the following shift from paradigm 7: *Activity by the sensitive photoperiod gene negatively controls the inherent capacity to develop to flowering*. An inherent capability for development to flowering is fully demonstrated by the lack of photoperiod control over days to flowering in peanut. In peanut, as in bean, the post-flowering photoperiod effect under long daylength is negative control over the inherent capacity to partition photosynthate toward the reproductive organs (yield accumulation).

*Paradigm 8. Photoperiod gene activity and its modulation by daylength are the major controls over time to flowering*

Paradigm 8 arises because the qualitative response to photoperiod has a much larger research and literature base (Vince-Prue 1975; Bernier 1988; Salisbury 1963; Salisbury and Ross 1981) than the interconnected controls by the several classes of other maturity genes and their modulations by temperature (Wallace et al. 1993a). Richards (1991) states: 'Crop phenology is the most important single factor influencing yield and adaptation'. Paradigm 8 can be correctly stated as: *Photoperiod and temperature are the primary environ-*

*mental controls over time to flowering and maturity, cultivar adaptation, and yield.*

A highly fragmented research and literature base (Nooden 1987; Hodges 1991) indicates that days to flowering is altered by interconnections between vegetative and reproductive growth. In addition to a delay in node to flower by enhancement of photoperiod gene activity as temperature rises, one interconnected effect on days to flowering is the need of more days for each node to develop as the temperature becomes lower (Wallace et al. 1991). A lower temperature causes a lower rate of node and leaf development prior to flower bud initiation (vegetative development is slower) (Hodges 1991). Flowering requires more days; i.e., rate of reproductive development (1/days) is lower. However, under low temperature (18°C), flowering in bean occurs at node 2–4 in contrast to occurring at node 10–12 at higher (28°) temperatures (Wallace et al. 1991). Thus, low temperature causes flowering to occur at an earlier stage of vegetative development (a lower node) than does high temperature. But, per unit time, the low temperature slows both vegetative and reproductive development. Genes that control the minimal node to flowering, number of nodes on shoots, and others aspects of plant habit are additional interconnected genetic controls over the days to flowering.

*We, therefore, propose seven paradigms*

- 1) Dependent on genotype and environment, photoperiod may control any or all stages of reproductive (yield) development by controlling the partitioning of photosynthate to support of growth of the reproductive organs versus continued growth of additional vegetative organs.
- 2) Depending on species and environment, competition can occur between any and/or all stage(s) of reproductive growth (yield accumulation) and the concurrent stages of vegetative growth and development.
- 3) The rate of reproductive growth (rate of yield accumulation) of a cultivar, plus the rate of vegetative growth prior to flowering, establish a cultivar's adaptation to the growing season duration of the site-season, and thereby strongly control the yield.
- 4) A non-promotive daylength negatively controls constituent capability for development toward flowering.
- 5) Daylength and temperature are the primary environmental controls over time to flowering and maturity, cultivar adaptation and yield.
- 6) In interaction with photoperiod, temperature synergistically controls photoperiod gene activity while simultaneously and interactively modulating multiple additional interconnected controls over rates of growth and development.
- 7) Dependent on genotype and environment, photo-

period can also control the partitioning to storage organs such as tuber, bulbs, and roots (yield) of certain crops.

*Complementary results from reductive combined with whole-system research*

As commonly conducted, yield trials of crop cultivars compare just the economic output of different genotypes. There is no attempt to elucidate variations of the physiological genetic mechanisms responsible for the differences in yield. The philosophical opposite to yield trials is basic research as commonly applied toward revealing biological mechanisms. The basic research approach, as Trewavas (1986) stated, is the reduction to intermediate levels of physiological processes such as photosynthesis or photoperiodism, plus the further reduction to molecular processes. The reduction is to isolate the processes studied, to prevent effects due to interaction with the system as a whole. This reductive research has resulted in the eight accepted paradigms presented above.

The subdivision of complex biological systems into components, as reductive research does, is essential to the elucidation of processes and mechanisms. We suggest additionally, however, that comparisons of the major components of the system with changes of the output (yield for example) of the system, as influenced by both genotype and environment, will more clearly elucidate the biological complexity.

The shifts suggested herein from the eight accepted paradigms were all derived from research that encompassed the entire yield system. System output (the yield) was compared against each of the smallest number of physiological components into which the system can be divided while still remaining inclusive of the entire system. This is the definition of a major component of the system. For the yield system, these major physiological components (Fig. 1; Fig. 1 of Wallace et al. 1993a; Fig. 3 of Wallace et al. 1993b) include: accumulation of the aerial biomass (process A), the output of which is the net accumulated biomass and is physiological component #1 of the yield; partitioning of a proportion of the biomass to the yield (process B), the obvious output of which is the harvest index, which is physiological component #2 of the yield; available photosynthate may be partitioned either to continuation of the vegetative growth (process C) or partitioned, alternatively, to initiation and continuation of growth of the reproductive organs (Process D). Due to competition for the same photosynthate, continued vegetative growth and continued reproductive growth must receive reciprocal proportions of the available photosynthate. The relative proportions will control the relative rate of growth of the reproductive organs versus the relative rate of

addition of more nodes and leaves, and stem or branch elongation.

Reproductive organs provide primary control over development (Nooden 1987) for the following reasons. Their rate of growth determines the time they need to develop to flowering and to maturity. Their short to long time to seed maturity will alter the time of hormonal influences from the seeds that initially intensify sink activity but shift toward causing senescence of the whole plant. This time to maturity becomes the duration across which biomass can be accumulated. The duration and rate prior to flowering establish the size of the vegetative structure that supports reproductive development (yield accumulation). The time between flowering and maturity becomes the duration of seedfill, the time across which both actual yield and harvest index accrue at calculatable average rates.

Elsewhere (Wallace and Masays 1988; Wallace 1991; Wallace et al. 1993a) we describe a yield system analysis that can be applied inexpensively to all yield trials conducted to guide the economic choice of which cultivar to grow. Yield system analysis measures all three major physiological components of yield: (1) aerial biomass, (2) harvest index, and (3) days to maturity. Additionally, yield system analysis subdivides each of these major components into the smallest number of subcomponents that remain inclusive of that entire component. Two subdivisions of time to harvest maturity (component 3, Fig. 1) are a pre-flowering duration of vegetative growth and a post-flowering duration during which any continuation of reproductive growth will be deprived of any available photosynthate partitioned toward any continuation of vegetative growth. The entire time to maturity facilitates calculation of the average rate of accumulation of biomass. The post-flowering time span facilitates calculation of the average rate of partitioning of part of the biomass toward yield.

Yield system analysis was applied to 51 bean yield trials (Wallace et al. 1992a). The comparisons between yield and its major components reinforced evidence obtained from inheritance studies (Wallace et al. 1993b). Both indicate control by photoperiod and other maturity genes over partitioning of the available photosynthate between continuation of reproductive growth and development versus continuation of vegetative growth and development. The partitioning of the photosynthate interconnects all three major physiological components of yield. Acceptance of these interconnections implies acceptance of the shifts described above from five of the eight accepted paradigms and rejection of three.

In addition to the above data for bean and peanut, data from the following 22 crops agree with the shifts in the paradigms. Recent publications show an

association of early maturity with high harvest index, and/or show photoperiod control over partitioning toward reproductive organs of yield or storage organs of yield such as tubers, bulbs, and roots. Such effects occur for soybean (Guiamet and Nakayama 1984; Settimi and Board 1988; Salado-Navarro et al. 1986; Yao et al. 1989; Lawn 1989; Morandi et al. 1990), sweet pea (Ross and Murfet 1985; Beverage et al. 1992), pea (Kelly and Davies 1988; Ross and Murfet 1985; Ross 1986; Beverage et al. 1992), wheat (Evans 1987), oat (Peltonen-Saino 1990; Salman and Brinkman 1992), pearl millet (Algarswamy and Bidinger 1985), gladiolus (Halevy 1987), clover (Boller and Nosberger 1983), radish (Keiller and Smith 1989), corn (DeLoughery and Crookston 1979), barley (Dormling et al. 1975), tobacco (Altamura et al. 1989), rice (Blanco et al. 1990), potato (Wolf et al. 1990), onion (Steer 1980), pigeon pea (Lawn 1989), mung bean (Lawn 1989), cowpea (Lush and Evans 1980); bambara groundnut (Linneman 1991); sorghum (Blum et al. 1989); and two flower crops *Chrysanthemum* and *Bougainvillea* (Kinet et al. 1985). For onion, the appropriate daylength for a cultivar causes partitioning of the photosynthate toward thickening of the leaves to form the economically valuable bulbs. Under an inappropriate daylength the photosynthate is partitioned toward growth of additional leaves. For potato, short daylength and/or low temperature cause partitioning toward the tuber rather than toward more stems and leaves.

Yield system analysis applied to all ongoing yield trials can inexpensively and progressively improve our understanding of interconnections among the physiological-genetic components of the accumulation of yield by crops. Neither highly reductive basic research nor yield trials alone can reveal these interconnections, just as yield trials combined with yield system analysis cannot elucidate molecular details. The improved knowledge provided by yield system analysis will complement mathematical modeling of crop management (Hodges 1991; Squire 1990), which is a complementary approach to research on whole systems. We suggest that accelerated elucidation of any complex biological system can result from combining highly reductive research with research on the whole system that includes relating the system output to the system's least reduced, most near-fully integrated components.

*Acknowledgements.* This research is a contribution to the W-150 regional bean research project. Financial support for this research from the Cornell University Experiment Station and from the USAID-funded Bean/Cowpea Collaborative Research Support Program is acknowledged.



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