Theor Appl Genet (1993) 86:27-40

© Springer-Verlag 1993

Improving efficiency of breeding for higher crop yield

D. H. Wallace[1,6], J. P. Baudoin[2], J. Beaver[3], D. P. Coyne[4], D. E. Halseth[6], P. N. Masaya[5], H. M. Munger[1,6], J. R. Myers[7], M. Silbernagel[8], K. S. Yourstone[6], and R. W. Zobel[9,1]

[1] Department of Plant Breeding and Biometry, Cornell University, Ithaca, 14853 NY, USA
[2] Facalte des Sciences Agronomiques, U.E.R. Phytotechnie des Regions chaudes, Gembloux, Belgium
[3] Department of Agronomy and Soils, University of Puerto Rico, Mayaguez, PR
[4] Department of Horticulture, University of Nebraska, Lincoln, Neb., USA
[5] Instituto de Ciencia y Tecnologia Agricolas, Guatemala City, Guatemala
[6] Department of Fruit and Vegetable Science, Cornell University, Ithaca, N.Y., USA
[7] Research and Extension Center, University of Idaho, Kimberly, Idaho, USA
[8] USDA-ARS, Irrigated Agriculture Research and Extension Center, Prosser, Wash., USA
[9] USDA-ARS, Department of Soils, Crops and Atmospheric Sciences, Cornell University, Ithaca, N.Y., USA

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

Summary. Exclusive selection for yield raises, the harvest index of self-pollinated crops with little or no gain in total biomass. In addition to selection for yield, it is suggested that efficient breeding for higher yield requires simultaneous selection for yield's three major, genetically controlled physiological components. The following are needed: (1) a superior rate of biomass accumulation. (2) a superior rate of actual yield accumulation in order to acquire a high harvest index, and (3) a time to harvest maturity that is neither shorter nor longer than the duration of the growing season. That duration is provided by the environment, which is the fourth major determinant of yield. Simultaneous selection is required because genetically established interconnections among the three major physiological components cause: (a) a correlation between the harvest index and days to maturity that is usually negative; (b) a correlation between the harvest index and total biomass that is often negative, and (c) a correlation between biomass and days to maturity that is usually positive. All three physiological components and the correlations among them can be quantified by yield system analysis (YSA) of yield trials. An additive main effects and multiplicative interaction (AMMI) statistical analysis can separate and quantify the genotype × environment interaction (G × E) effect on yield and on each physiological component that is caused by each genotype and by the different environment of each yield trial. The use of yield trials to select parents which have the highest rates of accumulation of both biomass and yield, in addition to selecting for the G × E that is specifically adapted to the site can accelerate advance toward the highest potential yield at each geographical site. Higher yield for many sites will raise average regional yield. Higher yield for multiple regions and continents will raise average yield on a world-wide basis. Genetic and physiological bases for lack of indirect selection for biomass from exclusive selection for yield are explained.

Key words: Yield physiology – Photoperiod/temperature – Partitioning – Harvest index – Maturity – Cultivar adaptation

Biological and theoretical bases of yield

Genetic × environmental effects

Genotype × environment (G × E) interactions determine the three major, genetically controlled, physiological components of yield: (1) the net accumulated biomass, (2) the harvest index, and (3) the time needed to develop to harvest maturity. Each component is an integration of numerous preceding biochemical and physiological steps. The three components integrate all effects on yield (Fig. 1; compare Fig. 3 and Table 2 of Wallace et al. 1993a and Fig. 1 of Wallace et al. 1993b).

Higher yield requires a larger biomass and/or a higher harvest index (Donald 1968; Evans 1983; Frankel 1947; Wallace and Zobel 1982; Gifford 1986, 1987; Frey 1988; Austin 1990; Lambers et al. 1990). Higher biomass requires a longer duration of growth

---

Correspondence to: D. H. Wallace

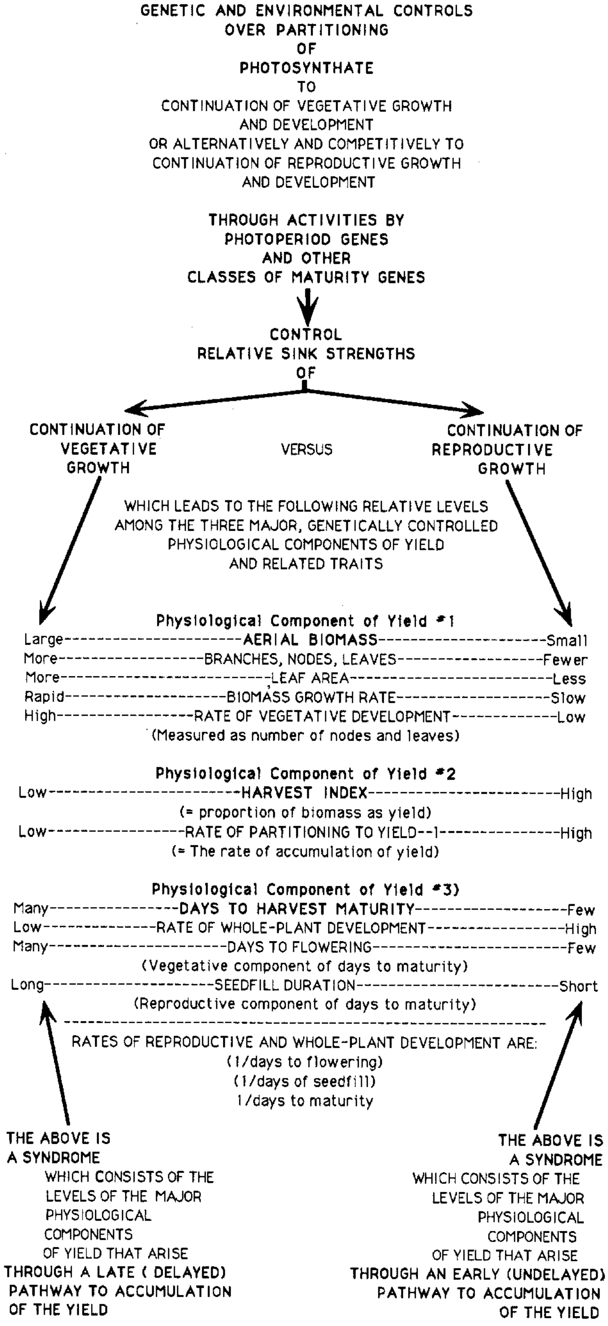

Fig. 1. Effects by alternative partitioning of photosynthate upon the three major, genetically controlled physiological components of yield and related traits (adapted from Fig. 3 and Table 2 of Wallace et al. 1993a)

and/or a higher rate of net photosynthesis. Higher harvest index requires a longer duration of growth of the organs that become yield and/or a higher rate of their growth. Consequences and biological bases for short to long times to harvest maturity are described below.

The time to harvest maturity that will give the highest yield depends on the environment and duration of the growing season. This environment establishes the growing season duration while, simultaneously, modulating most if not all gene activities (Fig. 1; Fig. 3 of Wallace et al. 1993a; Fig. 1 of Wallace et al. 1993b). The more the G × E interaction causes a time to harvest maturity that is neither shorter nor longer than the growing season, the better the cultivar is adapted to the environment and the higher the yield can be.

Environment and the duration of the growing season are physical factors. They become the fourth major physiological determinant of yield because they modulate and sometimes terminate the gene activities (Fig. 1; Fig. 3 of Wallace et al. 1993a; Fig. 1 of Wallace et al. 1993b).

Consequences of partitioning

For a seed crop, early vegetative growth leads to the first initiations of reproductive organs. Thereafter, the larger the proportion of the photosynthate partitioned toward them, the faster these organs will grow, the shorter the time they will require to develop to harvest maturity, and the higher both the rate of accumulation of yield and the harvest index will be. As compared with consequences from competitive partitioning of a larger proportion of the photosynthate toward continued growth of more shoots and leaves (Fig. 1), total biomass will be reduced due to both reduced leaf area plus the shortened duration of growth (Fig. 1; compare Fig. 3 and Table 2 of Wallace et al. 1993a).

A companion paper (Wallace et al. 1993a) and data herein verify for bean (*Phaseolus vulgaris* L.), and another companion paper (Wallace et al. 1993b) reviews for peanut plus gives citations for 22 other crops, the evidence that partitioning of the photosynthate results in negative or else positive correlations between all pairs among the three major, genetically controlled components of yield. It is shown that the G × E interaction caused by a single photoperiod gene, as modulated by daylength, can control the proportion of the photosynthate partitioned toward the reproductive organs (to yield accumulation) versus to continued growth of more branches and leaves (toward additional vegetative organs).

The partitioning of most of the photosynthate to the earliest initiated organs of yield will result in early maturity and high harvest index. This will give the highest yield if the growing season is short (Fig. 1, and Wallace et al. 1993a, b). Partitioning mostly toward continued growth of more branches and leaves provides the potential for higher yield than early maturing genotypes have, which can be realized if the growing season is long. Yield can be maximized if the time the genotype needs to develop to maturity matches the growing season.

The partitioning of photosynthate competitively (and quantitatively) toward the continued growth of already existing reproductive organs causes one syndrome of traits for early maturing cultivars (Fig. 1; Fig. 3 of Wallace et al. 1993a; Fig. 1 of Wallace et al. 1993b). Partitioning toward continued growth of more leaves and branches causes a contrasting syndrome for late cultivars. The syndromes consist of the negatively or else positively correlated changes in quantitative level among the three major components of yield, plus the rates of accrual of each component, plus additional correlations with the numbers of leaves, nodes, and branches, etc. The correlations among these traits result from control by photoperiod and other maturity genes over the competition for the photosynthate as well as from environmental modulations of these gene activities (Fig. 1; compare Figs. 3 and 1 of Wallace et al. 1993a, b, respectively). Large changes in gene activity result from variations in temperature and daylength (Squire 1990; Hodges 1991).

Differences in genotype, temperature, and/or daylength alter the relative sink activities of the above-described early and late pathways to highest yield (Fig. 1 and Wallace et al. 1993a, b). The early pathway results from the predominant continuation of reproductive growth; the late pathway results from the initial predominance of continuation of vegetative growth. Every site has a range of variation in temperatures and/or moisture regimes for the same season of successive years, which results in year-to-year variation of the growing season duration. Therefore, invariably, two or more genotypes (cultivars) are recommended for a site, to allow for the shorter-than-average, intermediate, and longer growing season durations.

Environmental variation, including its consequent range of season duration, plus the range of genotypes grown cause quantitative variation of the G × E interaction. Quantitatively variable G × E results in a continuum between the extremely early and extremely late pathways to yield. An extremely late pathway is represented by bean cultivars that use 6–9 months to mature at tropical highland sites at a low temperature. The extremely early pathway to yield is required at temperate sites with a duration of highest temperatures that give growing seasons of 60–90 days and also at tropical sites with similarly short rainy seasons. Most geographical sites have growing seasons intermediate between these extremes. Data will be presented which suggest that the highest yield of successive growing seasons at a repeated time of year and same site results from the early pathway to yield for about half of all years but from the later pathway for the other half.

Interpretation that the proportion of the photosynthate partitioned to the already existing reproductive organs controls both the rate of accumulation of yield (compare Fig. 1) and the time needed to develop to harvest maturity was introduced recently (Wallace 1985; Yourstone and Wallace 1990; Wallace et al. 1993a, b). At first consideration, that the rate of yield accumulation determines the days needed to develop to maturity seems opposite the concept that the days to maturity determines the cultivar adaptation and thereby controls the yield. This paradox is explained by feedback plus feedforward interconnections among the three major components of yield; some of both of these result from quantitative variation of the partitioning (Fig. 1 and Figs. 3 and 1 of Wallace et al. 1993a, b respectively).

Measurement of development

Vegetative growth is an increase in biomass; vegetative development is an increase in number of nodes and attached leaves (Fig. 3 of Wallace et al. 1993a; Torigoe 1986; Squire 1990). Each additional leaf increases both the capacity for photosynthesis and the number of nodal positions where organs of yield (buds, fruits, and seeds) can be initiated.

The growth and development of existing buds, fruits, and seeds do not increase their number, so the continued development of reproductive organs can be quantified only by its rate. Summerfield and Roberts (1988) (see also Squire 1990) describe this rate as the reciprocal of the time used to develop to the referenced developmental stage, such as 1/days to flowering and 1/days to harvest maturity. They state: 'The reason an event happens in a short time is because the rate of progress was rapid, and not vice versa'. This agrees with the hypothesis (Fig. 1; Figs. 3 and 1 of Wallace et al. 1993a, b) respectively and evidence that (a) the time required to complete development to flowering is controlled by the rate of growth of the flower buds; after which (b) the time required to complete development to harvest maturity is further controlled by the rate of growth of the pods and seeds.

The interception of more light energy or its more efficient conversion to biomass can increase the available photosynthate. This may raise the rate of partitioning to the yield, without altering the partitioned proportions (Fig. 1). The rate of biomass accumulation and the rates of vegetative growth and development plus the rate of accumulation of yield would all be higher. However, any continuation of more vegetative growth due to any environmental or genetic enhancement will tend to delay development to harvest maturity (Fig. 1; Figs. 3 and 1 of Wallace et al. 1993a,b respectively).

Previous selection for physiological traits

Disappointing yield gains have arisen from selecting for net photosynthesis, nitrogen fixation and utilization, photo- and dark-respiration, light interception, leaf chlorophyll content, and for activity of enzymes in the pathways of photosynthesis and nitrogen utilization (Apel 1984; Black and Burris 1975; Evans 1983; Gifford 1986, 1987; Harper et al. 1985; Hayashi 1969; Jordan and Ogren 1983; Rasmusson 1987; Wallace 1980; Zelitch 1971; Mahon 1990; Lambers et al. 1990). Gifford (1987) concluded tht selection for rate of photosynthesis will not lead to higher yield until we understand 'feedback regulations arising from environmental limitations in the field'. These are the environmental effects on the G × E interaction.

Wallace et al. (1976), Wallace (1980), and Wallace and Zobel (1982) reported that statistically significant differences between genotypes for net CO_2 exchange rate (NCE) can be identified easily. However, in crosses between genotypes with high and low NCE, correlation between the NCE of an F_2 segregate and the mean NCE of its F_3 progeny was 0.07. Correlation with yield was lower. Consequently, the cited papers suggested that selection for physiological traits will fail to assist breeding for higher yield if their gene actions occur far in advance of the actual accumulation of the yield. Wallace and colleagues suggested that failure occurs because these gene activities interact with too many other segregating gene effects and physiological processes; the numerous interconnections among parts of the system cause their genetic influence to become unpredictable. Similarly, Mahon (1990) indicates that control over NCE by many genes makes it impossible to achieve the 'all else being equal basis' required to determine the inheritance of differences in NCE.

Wallace (1973, 1980), Wallace et al. (1976) and Wallace and Masaya (1988) suggest that effective indirect section for yield should result from selection for the three major physiological components of yield (biomass, harvest index, and days to maturity) since each has already integrated all of the relevant gene actions, environmental influences, and G × E interaction effects. The present paper emphasizes the necessity of simultaneous selection for all three components, plus selection for the specific G × E interaction that is best adapted to each different target environment. Selection for rate of accumulation of both biomass and yield are needed most because, for reasons explained in following sections little if any indirect selection for biomass results from selection for yield.

Control over partitioning by maturity genes

The hypothesis that partitioning of the photosynthate controls the time the genotype uses (needs) to develop to harvest maturity arose from attempts to combine high harvest index with high biomass (Wallace et al. 1993a, b). The papers reporting these attempts verify that a photoperiod gene can interact with daylength to control simultaneously the harvest index and the days to both flowering and maturity. The original breeding objective was the 50% higher yield achievable if the higher harvest index of an early parent was successfully combined with the larger aerial biomass of a late parent. Segregates that inherited high harvest index were always both early and photoperiod insensitive. Their higher accumulation of yield per day resulted in the same yield in about 85 days as the late and photoperiod-sensitive segregates give in 105 days. Replacing the insensitive genotype with the sensitive one results in a delay of flowering by both longer daylength and higher temperature, attended by enlarged biomass but lowered harvest index (Wallace and Enriquez 1980; Wallace et al. 1991; Wallace et al. 1993a; Masaya and White 1991).

Although not discussed while reviewing environmental effects on partitioning to yield (Synder and Carlson 1984) and barely referred to in more recent reviews of partitioning (Lawn 1990; Wardlaw 1990; Lambers et al. 1990), many investigators independently present data that either show an association of high harvest index with early maturity or are interpretable as control over this partitioning by daylength. Wallace et al. (1993b) cite such reports of 22 crops in addition to beans. Squire (1990) also describes effects by daylength on the harvest index. Also, higher temperatures cause large quantitative increases in days to flowering and maturity for photoperiod-sensitive genotypes if daylength is intermediate, and synergistically larger increases if the day length is also extended (Gniffke 1985; Wallace and Enriquez 1980; Wallace et al. 1991).

Yield system analysis

We propose that efficiency of breeding for higher yield can be raised by applying a yield system analysis (YSA) to ongoing yield trials. A complete YSA (Wallace and Masaya 1988; Wallace 1991) measures: (1) days to flowering, (2) days to maturity; (3) the aerial biomass at harvest maturity, and (4) the yield (Table 1). Calculated from these (Table 1) are: (5) days of seedfill (days to maturity minus days to flowering), (6) average rate of yield accumulation per day to maturity (the economically relevant average partitioning rate to reproductive growth), (7) the average rate of yield accumulation per day of seedfill (the physiological origin of the economic rate), (8) the rate of accumulation of aerial biomass averaged across the days to maturity (this measures the average crop growth rate and net photosynthetic efficiency), and (9) the harvest index, which is yield biomass divided by aerial biomass (this ratio quantifies the consummated partitioning).

The eight traits measured by YSA in addition to

Table 1. Nine outputs from the yield system of a cultivar

Trait No.	Output	Interpretation	
	Four direct measurements within each yield trial		
1	Days to flowering	Time used for development to flowering	
2	Days to harvest maturity	Time used to develop to harvest maturity	
3	Aerial biomas	The overall net photosynthesis	
4	Yield	The economically important output	
	Five calculations from the four direct measurements		
5	Days of seedfill	Time used for actual yield accumulation	
6	Yield/day to maturity	Efficiency of yield accumulation	The rate of partitioning
7	Yield/day to seedfill	Efficiency of yield accumulation	
8	Biomass/day of plant growth	Efficiency of photosynthesis	
9	Harvest index	Endpoint efficiency of partitioning to yield	

yield include yield's three major, genetically controlled components: the net accumulated biomass (YSA trait #3), the harvest index (YSA trait #9), and the days to harvest maturity (trait #2). The other five traits encompass all the major subcomponents of all three major components. Inferred by major is that the trait cannot be subdivided into fewer components; division into subcomponents increases the number. The duration of growth (YSA trait #2) and the average biomass accumulated per day of growth (trait #8) are the two subcomponents of the net accumulated biomass (trait #3). The two subcomponents of harvest index (trait #9) are the duration of seedfill (trait #5) and the average rate of partitioning (rate of accumulation of yield) per day of seedfill (trait #7). Compared with the rate per day of seedfill, the average rate of yield accumulated per day of plant growth presents the true economic viewpoint rather than the physiological one. Two subcomponents of time to harvest maturity are the pre-flowering and post-flowering durations. These are the vegetative and reproductive stages, respectively; the latter being the duration of seedfill (trait #5).

Additional measurements could be incorporated into YSA. For example, a measurement not included above is the biomass at flowering. Measuring it would differentiate quantities and rates of biomass accumulation during the vegetative stage from the respective quantities and rates during the reproductive stage. It would more completely separate the rate and duration of biomass accumulation of the reproductive stage from the simultaneous rate and duration of partitioning.

Ascertaining the yield potential of a genotype requires its comparison with other genotypes across multiple yield trials because the G × E interaction is altered by each different environment, even by small differences between successive seasons at the same site and time of year. Yield trials will always be required to identify the best cultivars for growers. The application of YSA to each yield trial compares the differences in gene action among the cultivars within that site-season (a specific environment) (Scully and Wallace 1990, 1991). Comparisons of YSA traits across repeated seasons at a site will identify the earliest to latest maturities and the G × E interactions with adaptation to that site. It will quantify average correlations between these maturities and the aerial biomass and harvest index plus their rates and durations of accumulation.

Effects on yield and its physiological components and their subcomponents by fertilizer, irrigation, chemical control of diseases and insects, etc. arise through environmental influences on the G × E. YSA can quantify the physiological-genetic bases of yield differences due to altered levels of such abiotic and biotic factors, or other agronomic treatments.

The measurement of actual total biomass is needed to improve the efficiency of breeding for higher yield. The truly essential need is the identification of genotypes that have the highest average rates of accumulation of biomass and their subsequent use as parents. These can be identified accurately enough by measurements of the relative aerial biomass and the duration of its accumulation. With care, fresh weights of aerial organs may be an adequate measurement for some crops. Leaves that abscise prior to maturity can be ignored because leaf biomass is correlated with the remaining aerial biomass. Leaves that remain on some genotypes at harvest can be removed to improve the uniformity of comparison among the genotypes. A costly measurement of root biomass is also not essential because of its usual correlation with aerial biomass (Russell 1977).

Yield system analysis (YSA) incorporates the following eight concepts:

1) indirect selection for yield will be most effective when applied to processes which have already integrated most of the genetic and environmental effects that lead to yield. The selection will be for

the processes and traits that implement actual accumulation of the yield.

2) Levels of each major component of yield will be correlated with the yield in most yield trials. However, the levels and negative versus positive correlation will vary with the developmental stage(s) of the plants when stresses or favorable environments occur.
3) Almost every newly incorporated or excluded gene activity may cause G × E interaction that will affect yield and/or its physiological components (Blixt and Vose 1984).
4) Almost every change in the level of an environmental factor may cause G × E interaction that will alter yield and/or its physiological components.
5) Within the environment of each yield trial, the variability for a component among the tested cultivars will quantify variation in the genetic control over that component.
6) The variations of yield and its components expressed by a genotype across environments of multiple seasons (at the same or different sites) will quantify the control by differences in the environment (Blixt and Vose 1984; Mayo 1987; Zobel et al. 1988).
7) The superior levels measured for each YSA trait indicate adaptation of the genotype to the tested environment.
8) Measurement must be economically feasible for the large number of genotypes, progenies, and environments required for effective selection.

Results from yield system analyses

In this paper, YSA is discussed for a seed crop. With modifications, YSA is applicable to root and tuber crops (Wolf et al. 1990) and other crops for which only part of the plant is the yield.

Four sets of yield trials

YSA was conducted in New York on red kidney bean breeding lines for which, as described above briefly and in detail in Wallace et al. (1993a), most of the maturity differences and differences in harvest index were due to the insensitive versus sensitive allele of a single photoperiod gene. Days to maturity, yield, and aerial biomass were measured beginning in 1981, measurement of days to flowering began in 1987.

New York's bean variety testing program applied YSA from 1985 through 1988. Each year about 40 commercial or improved genotypes were compared. Several commercial bean classes were always represented.

An International Bean Flowering and Adaptation Nursery was distributed by Centro Internacional de Agricultura Tropical, Cali, Colombia. From 1983 to 1984, 48 cultivars from 15 countries were compared. Known ranges of sensitivity to photoperiod, adaptation to temperature, and plant habit were spanned. Four trials were in Colombia, 4 in New York, 2 in Puerto Rico and Nebraska, and 1 in Peru, Belgium, and Canada (Yourstone 1988). Yield, days to flowering, and maturity were measured at all sites; aerial biomass was not measured at 5 sites. YSA was done for the genotypes that produced yield at all environments.

A Cooperative Dry Bean Nursery is coordinated annually by the University of Idaho (Myers 1988). Each year the 30–40 cultivars include most commercial classes. At one site all of the four traits needed for complete YSA were measured in 1985; this was carried out at 8 sites in 1987 and 1988. All traits except days to flowering were measured at 6 other sites. The sites were in Alberta, California, Colorado, Idaho, Kansas, Nebraska, Michigan, Montana, North Dakota, Washington, and Wyoming.

The above-described four sets of yield trials measured yield and days to maturity in 51 environments (site-seasons); days to flowering was measured in 31, aerial biomass in 33, and both in 23. For each environment the Pearson-product moment correlation was calculated between each of the 36 pairs among the nine YSA traits measurable (Table 1) when days to flowering, days to maturity, aerial biomass, and yield are all recorded. Within the environment of each yield trial, correlation between traits suggested simultaneous control by the genotype. The results were summarized (Table 2) as the average of all the single correlations within the individual environments and by chi-square analysis of whether, across all tested environments, the number of positive correlations differed significantly from the number of negative correlations.

Correlation of partitioning with time used for development

Across 33 environments for which measurement of aerial biomass made it possible to calculate the harvest index, harvest index was on average negatively correlated (Table 2) with days to flowering ($r = -0.17$), seedfill duration ($r = -0.23$), and days to maturity ($r = -0.45$). The -0.45 was lower than the $r = -0.75$ for eight trials held in New York of red kidney been breeding lines that all had the same determinate plant habit with six to eight nodes on their main stem. These lines had early versus late maturity which, respectively, were controlled by the insensitive and a sensitive allele of one photoperiod gene (Wallace et al. 1993a). Removing these eight trials from the comparison

Table 2. The average correlation between all possible pairs among nine output traits from the yield system, measured across 20 to 51 yield trials. The yield trials were conducted in 12 different US states, two Canadian provinces, plus Puerto Rico, Peru, Colombia and Belgium

	Days used for development to indicated stage or by that stage			Rate of accumulation of the indicated biomass			Biomass and its partitioning to vegetative versus reproductive growth	
	Flow	Matu	SdFi	Yd/D	Sf/D	Bi/D	Biom	Haln
Yield	0.07	0.01	−0.01	0.93	0.84	0.72	0.70	0.54
Probability that the number of positive and negative correlation is equal when yield system analysis of many yield trials are considered	0.37 IND	0.48 IND	0.578	zero	zero	zero	0.00	0.0001
Days to flowering		0.66	−0.11	−0.01	0.07	0.11	0.30	−0.17
Probability of equal number of positive and negative correlations as determined by chi-square analysis		0.00 IND	0.095	1	0.194	0.179	0.002 IND	0.016 IND*
Days to maturity			0.57	−0.27	−0.16	−0.07	0.34	−0.45
Probability of equal number of positive and negative correlations			0.0002	0.0001 *	0.131	0.157	0.002 IND	0.0001 IND**
Days of seedfill				−0.14	−0.3	−0.19	0.04	−0.23
Probability of equal number of positive and negative correlations				0.336	0.001	0.398	0.655 IND	0.025 IND**
Yield per day of plant growth					0.92	0.76	0.54	0.67
Probability of equal number of positive and negative correlations					0.0001	0.0001	0.0001 IND	0.0001 IND**
Yield per day of seedfill						0.73	0.59	0.69
Probability of equal number of positive and negative correlations						0.0001	0.0001 IND	0.0001 **
Biomass per day							0.86	0.21
Probability of equal number of positive and negative correlations							0.0001	0.003
Total biomass								−0.05
Probability of equal number of positive and negative correlations								0.602
Harvest index								–

IND = Measurements of the correlated traits are done independently so calculation does not arithmetically introduce autocorrelation; all other correlations include some auto-correlation

For interpreting the biological cause of the correlations, cells with * or ** are the most informative

lowered the average correlation of harvest index with days to maturity to −0.20. This still negative correlation was the average across 25 tropical and temperate environments and across cultivars that originated from multiple breeding programs at widely dispersed geographical locations. In spite of these diverse environments, a large range in numbers of nodes on the shoots and variations in plant habit, all of which partially control times to flowering and maturity (Wallace 1991; Wallace et al. 1993a, b), only 1 of all 33 trials had positive correlation between days to maturity and harvest index. This site had negative correlation for the different environment of the same season of another year. Chi-square analysis indicated 1 chance in 10,000 that the true average biologically caused correlation between days to maturity and harvest index (partitioning) is not negative, and 2 or 3 chances in 100 that the true average correlations between harvest index and both days to flowering and days of seedfill are not negative (Table 2). These are valid probabilities for a biologically caused correlation because the procedures used to measure biomass and time are fully independent.

Biologically-caused versus autocorrelations

The average correlation of yield with yield per day to maturity was $r = 0.93$ (Table 2); the average correlation of yield with yield per day of seedfill was $r = 0.84$. The calculation introduced auto-correlation into both correlations because yield is a component of both of the variables. The auto-correlations invalidate the assumption that the average correlations are the true biologically caused correlations. Auto-correlations do not, however, invalidate the obvious consequence that partitioning of the photosynthate controls the rate of yield accumulation or the hypothesis that the proportion partitioned to the reproductive (yield) organs controls the time to harvest maturity (compare Wallace et al. 1993a, b).

Correlation of yield with its biomass components

Yield had a positive average correlation with aerial biomass ($r = 0.70$); average rate of aerial biomass accumulation (0.72), harvest index (0.54), and the average rate of partitioning to reproductive growth based on both days to maturity (0.93) and days of seedfill (0.84) (Table 2). The latter two correlations were the highest, and their ranges were the smallest (1.00–0.72), in part because both include auto-correlation. It is possible for yield to be negatively correlated with either biomass or harvest index, but both anomalies occurred for only 1 out of 33 yield trials. The true average correlations were positive ($P = 0.0001$).

Correlation of yield with developmental time

The correlation of yield with days to maturity was positive for about one-third of 51 environments, often being statistically significant. The correlation was negative and often significant for another third, and was near zero for the last third. The range was $r = 0.70$ to -0.74. The average (0.01, Table 2) did not differ significantly from zero. Positive and negative correlations of yield with days to flowering and with days of seedfill also occurred with near-equal frequency. Time in days and yield in grams are measured independently, so auto-correlation is not incorporated. These data indicate that while the days to maturity strongly controlled cultivar adaptation and thereby controlled the yield for about two-thirds of the environments (yields trials) about half of all of the 51 site-seasons (environments) caused a negative correlation while half caused a positive correlation (Table 2). The time to maturity that maximized yield varied from site to site. Even at the same site, for the same season of different years, yield was highest for the earlier cultivars for 1 year but highest for later cultivars for other years.

For 6 tropical environments (latitudes 2, 3, 6, and 18°) of the International Bean Flowering and Adaptation Nursery, the correlation of yield with maturity averaged 0.25. This supports the conclusion (White and Izquierdo 1989) that, at tropical sites with short daylength and lack of stress(es) which terminate the growing season, a longer duration of growth and development will increase yield. Seven temperate-zone site-seasons (latitudes of 41, 42, and 50°) had an average correlation of -0.10.

Twelve temperate-zone site-seasons of the Cooperative Dry Bean Nursery had a negative correlation and 15 had a positive correlation between yield and days to maturity. The range was $r = -0.69$ to 0.70. Four of 6 sites with yield trials for 2 years had a negative correlation for 1 year but positive for the other. A 7th temperate site, the New York trials with early maturing insensitive versus late photoperiod-sensitive red kidney breeding lines, and with these maturity differences controlled by one photoperiod gene (Wallace et al. 1992a), had a negative correlation for 6 years (average -0.34) but a positive one for 2 years (average 0.20).

In New York, higher than usual temperatures plus adequate moisture during the early growing season of some years allow exceptionally vigorous vegetative growth. For photoperiod-sensitive cultivars a higher temperature delays flowering and maturity more than usual by amplifying the delay in flowering caused by the long daylength of the growing season of every year. Intensification of photoperiod gene activity by high temperature (Wallace and Enriquez 1980; Gniffke 1985; Wallace et al. 1993a, b; Yourstone and Wallace 1990) is one explanation of why yield can be the highest for early maturing cultivars for some seasons and the highest for later maturing cultivars for other years (Figs. 3 and 1 of Wallace et al. 1993a, b, respectively). Nevertheless, the yield may not be the highest for later cultivars for years when moisture availability has facilitated accumulation of larger than usual biomass, if variations in late-season temperatures and early to late frosts, and/or variable moisture regimes result in environments and/or growing season durations that do not advantageously use the time to maturity caused by the temperatures and daylength of the earlier part of the season. Temperature and moisture variations accelerate to slow or sometimes abruptly stop yield accumulation and development to maturity (Wallace et al. 1993a, b).

Interaction of vegetative × reproductive development

Except when excessively high, a higher temperature will cause genotypes of beans that are photoperiod insensitive (Wallace and Enriquez 1980; Gniffke 1985; Wallace et al. 1993a; Yourstone and Wallace 1990) and insensitive genotypes of other crops (Wallace 1985; Tollenaar and Hunter 1983; Craufurd and Biddinger 1988; Summerfield and Roberts 1988) to flower and mature in fewer days. Earlier flowering occurs because the higher temperature accelerates vegetative development so that fewer days are needed to develop a node. Photoperiod-insensitive genotypes have minimal photoperiod gene activity. Therefore, higher temperatures will cause minimal if any delay of the node to flower.

In contrast, for a photoperiod-sensitive genotype under delaying daylength, a higher temperature will amplify the photoperiod-gene implemented delay of node to flower (Wallace and Enriquez 1980; Wallace et al. 1991), which causes a propensity toward later flowering. Simultaneously, as for the insensitive genotypes, the higher temperature reduces the days required to develop each node (Wallace et al. 1991), which causes in the same plant a propensity toward earlier flowering. The opposing propensities become equal and each cancels the other at the optimal temperature for flowering. This optimum is at the bottom of the U-shaped response of days to flowering to temperature (Wallace et al. 1991). If the temperature is above the optimum for flowering, the propensity to flower in fewer days as the temperature rises is masked by a larger propensity for delay of flowering, (Wallace et al. 1991). on the contrary, the propensity to need more days to develop to flowering as the temperature rises is fully masked by a larger propensity to flower earlier if temperatures are below optimum for flowering. These G × E interactions include the lowering of the optimum temperature for flowering by both longer daylength and a genotype with higher sensitivity to photoperiod (Wallace and Enriquez 1980; Wallace et al. 1991). Temperatures that rise sufficiently can amplify even the minimal photoperiod gene activity of an insensitive genotype enough that its masked delay of flowering becomes as large as the reduction of days due to the shorter time needed to develop a node caused by the higher temperature. The then equal propensities constitute the optimum temperature for flowering. Any further rise in the temperature will delay the flowering (Wallace et al. 1991).

Our hypothesis is that temperature acceleration of photoperiod gene activity delays the node to flower by reducing the amount of photosynthate partitioned toward continued growth of the earliest initiated flower buds, (Figs. 3 and 1 of Wallace et al. 1993a, b, respectively). This agrees with the classification of beans as insensitive for initiation of flower buds but sensitive for continued growth and development of the buds (Salisbury and Ross 1991). A sufficient reduction in the photosynthate partitioned to the existing buds causes them to abort, thereby delaying both the node and the days to flowering (Wallace and Enriquez 1980; Wallace et al. 1993a, b; Yourstone and Wallace 1990). The delay of node will be synergistically enlarged with increases of both temperature and daylength (Wallace et al. 1991). The photosynthate not partitioned to the already initiated reproductive organs is available for and will accelerate the growth of more branches and leaves (Fig. 1). This continued vegetative growth will increase the potential number of buds, flowers, pods, and seeds (organs of yield) at later developed nodes (Wallace et al. 1993a, b).

Photoperiod genes interact with additional classes of maturity genes. One class affects days to flowering by controlling the rate of vegetative (node) development (Fig. 4 in Wallace et al. 1991). Another class establishes the number of nodes on the plant's main shoot and branches (Wallace et al. 1991). Yet another class controls the earliest node with the potential to produce a flower (Murfet 1977). Some crops have a class called vernalization genes. They control time to flowering via a required duration of exposure to 'low' temperature (Hoogendorn 1985; Ross and Murfet 1985). Interactions among the classes of maturity genes and their differential responses to daylength and/or temperature result in complex G × E interaction effects on days to flowering and maturity (Syme 1973; Wallace et al. 1993a, b). Knowledge of maturity-gene classes and their effects on the G × E interaction can be applied toward increasing the number of segregates from crosses that have a days to maturity adapted to the site and toward creating planned combinations of maturity, harvest index, biomass, and higher yield.

Strategy for breeding for higher yield

Selection for biomass must accompany selection for yield

Exclusive selection for yield always results in indirect selection for days to maturity because the highest yield tends to occur for genotypes that require neither fewer nor more days to maturity than the growing season. Selection at the same site for the repeated season of multiple years will eliminate genotypes that mature in a shorter or longer time than the shortest and longest season durations at the site. Each year there will be indirect selection for the season's shorter, intermediate, or longer duration. Indirect selection for maturity will also result in an indirect selection for harvest index because it is controlled by the maturity genes (Fig. 1 and Wallace et al. 1993a, b).

Control over the three major physiological components of yield is divided between only two overlapping groups of genes. The few maturity genes become integral to the control over total biomass by all genes by directing partitioning of the photosynthate either toward growth of more shoots, branches, and leaves or toward rapid (and current rather than later) accumulation of yield (Fig. 1; Figs. 3 and 1 of Wallace et al. 1993a, b respectively). After a cross, the occurrence of a genotype that breeds true for a higher harvest index requires a superior segregate from recombinations among the comparatively few maturity genes. The occurrence of true-breeding higher biomass requires the genotype to arise from segregation and recombination among virtually all of the plan's thousands of genes, including the maturity genes. The probability for a true breeding genotype with higher biomass is very low; biomass has extremely low heritability. Comparatively, harvest index and days to maturity have very high heritabilities.

The many fewer segregates that breed true for higher biomass than harvest index are a genetic explanation of why, for self- and open-pollinated crops, selection for higher yield has raised it through a higher harvest index with little if any gain in total biomass (Austin 1990; Gifford 1986; Squire 1990; Lambers et al.

1990; Blum et al. 1991). A further physiological explanation is that the effective indirect selection for days to maturity becomes indirect selection for harvest index also, since both are controlled by the maturity genes. Minimal if any indirect selection for total biomass plus differences in range of growing season duration and environment between sites and between successive but comparable seasons at the same site dictate the following: the deliberate selection of genotypes that have higher rates of accumulation of biomass and their subsequent use as parents are essential to obtaining maximized progress from breeding for higher yield.

Robertson and Frey (1987), Takeda and Frey (1987), and Frey 1988 raised yield in oats by selecting for higher biomass. They considered higher rate of biomass accumulation to be the only option for higher yield because the days to maturity of existing cultivars already matched the short growing season and harvest index was already high enough that enlarging it would be detrimental to yield. There should also be selection for a higher rate of accumulation of yield per day to compensate for the tendency for the higher biomass to arise from longer duration of growth.

Crops which use hybrid varieties benefit from heterosis. Heterosis can result in indirect selection for total biomass from selection for yield (Tollenaar 1991; Blum et al. 1991).

The positive correlation of bean yield with aerial biomass ($r = -0.70$, Table 2) would seem to suggest the potential for indirect selection of biomass by selection for yield, but the range of this correlation was 0.98 to 0.23, plus a negative correlation of -0.23 for 1 of the 33 yield trials. Correlation of yield with biomass tended to decrease as the correlation with harvest index increased. The average correlation of 0.54 between yield and harvest index also included 32 positive and 1 negative correlation; the range was 0.87 to 0.03 plus the single negative correlation of -0.27. Biomass and harvest index were negatively and positively correlated with near-equal frequency, the range being $r = -0.72$ to 0.68. The average was -0.05.

Long-term exclusive selection for yield will gradually exploit all of the useful genetic variability for harvest index and days to maturity (Frey 1988; Austin 1990). It will lead toward an excessively high harvest index because a smaller vegetative structure must support larger yield without causing lodging that will reduce canopy photosynthesis. After accrual of these negative consequences, exclusive selection for yield can raise it only through indirect selection for higher biomass. Indirect selection for higher biomass cannot occur if genes for superior biomass are not introduced through the parents of crosses. The measurement of aerial biomass is the most costly step of YSA. The current inefficiency in exclusively selecting for yield, and that its continuation will progressively further decrease its efficiency, suggest higher long-term costs from not measuring the biomass now. That the biomass can be measured in yield trials already being conducted for variety selection minimizes the cost.

Selection solely for larger biomass will tend to give a later maturity and lower harvest index and yield. Selection solely for higher harvest index will lead toward early maturity, with the consequent lowering of yield as reported by Kenworthy and Brim (1979), Robertson and Frey (1987), Takeda and Frey (1987), and Werner and Wilcox (1990). Selection solely for earlier maturity will reduce both biomass and yield. Negative indirect effects from exclusive selection for each component implies superior effectiveness from simultaneous selection for yield plus all three of its major physiological components and their subcomponent durations and rates.

G × E effects on photoperiod responses

The photoperiod-gene class of maturity genes is so responsive to quantitative variations of daylength and temperature (Wallace and Enriquez 1980; Wallace et al. 1993a) that most early research reports concluded maturity was controlled by many genes. Recently, quantitative variations of days to flowering and maturity are interpreted as being controlled by a few genes (Murfet 1977; Wallace 1985; Wallace et al. 1993a, b). Most crops with sensitivity to daylength have a 'quantitative photoperiod response'; times to flowering and maturity are progressively enlarged as the daylength is progressively longer (for short-day plant species) or shorter (for long-day species). This contrasts with the 'qualitative photoperiod response' preferred for laboratory and molecular studies of photoperiodism (Bernier 1988; Kinet et al. 1985; Vince-Prue 1975; Vince-Prue et al. 1984; Wallace et al. 1993b). Qualitative response indicates that the genotype (usually identified by species only) has photoperiod genes which are so sensitive that one or a few short or long days completely induces or inhibits flowering.

Traditional breeding for yield

In addition to selecting for yield breeders often select for a set of whole-plant traits they believe likely to raise yield. The collective set of traits is called an ideotype (Blixt and Vose 1984; Donald 1968; Kelly and Adams 1988; Rasmusson 1987; Sedgley 1991). Rasmusson (1987) summarized as follows. A traditional breeder seeks to enhance genetic potential for yield by selecting for yield per se, plus by selection for individual traits. Identifying individual traits which will enhance yield universally or even in a relatively limited genetic and climatic situation is difficult.

Measuring and selecting for G × E interaction

The inability to interpret, quantify, and select directly for that G × E interaction which will maximize yield for the narrowed range of environments at each production site has also constrained genetic advance in yield (Zobel 1990; Kang 1990). Yield trials of multiple genotypes grown across multiple environments are required to quantify this G × E, to determine how the G × E effect is altered by each genotype and each environment, to determine the yield potential of each genotype, to determine the optimum balance of levels among the major components of yield for each site, and to select for adaptation to the range of environmental variation at that site (Wallace et al. 1993a, b). Zobel et al. (1988) and Gauch (1988, 1992) have developed an additive main effects and multiplicative interaction effects (AMMI) statistical model. For yield trials conducted at three or more environments, AMMI analysis can quantify the effect on the G × E interaction caused by each genotype and separate it from the G × E due to each environment (Crossa 1990; Gauch 1992). AMMI does this by applying principal component analysis to the G × E sums of squares of an ANOVA. This quantifies the positive or negative deviation around the grand mean yield across all the environments (multiple yield trials). If YSA has been applied to the yield trials, AMMI can also quantify the G × E-caused deviation for each of yield's major components and subcomponents that is due to each genotype and to each environment.

Application of YSA-AMMI analysis to yield trials conducted across a region reveal large G × E interaction effects (Wallace et al. 1991). Yet larger G × E occurs across the broader environmental variabilities of multiple regions. First-time perception of smaller G × E interactions within sites and regions can be assisted through measurement of G × E across broad ranges of environments and genotypes. YSA-AMMI can also facilitate mathematical modeling of plant development and yield (Charles-Edwards and Vanderlip 1985; Whisler et al. 1986) and its application to improving crop breeding and production practices.

Conclusions

The first task of breeding

Simmonds (1989) indicates that the first task of efficient breeding is the creation of superior genetic segregates. We suggest larger numbers of higher yielding segregates can result from applying YSA-AMMI to yield trials. YSA-AMMI will identify the genotypes that accumulate the largest biomass per day, rather than those that just grow for a longer time, and the genotypes with highest harvest index due to either a higher rate of partitioning and/or a longer duration of seedfill. Highest yield will indirectly identify the optimal maturity. There will be more than one optimal maturity (or a range thereof) if the successive but comparable growing seasons at a site vary in duration, since some cultivars can maximize yield for the shorter seasons through a high rate of yield accumulation and high harvest index, while others optimize for the longer than usual season through longer vegetative growth and lower rates of actual accumulation of the yield. Superiority for yield and/or each of its components demonstrates superior adaptation to the specific environment of the site-season. The selection of all these superior genotypes across the shortest to intermediate to longest of the repeated growing seasons will assemble a range of genotypes with demonstrated adaptation to the site. Genotypes that are both adapted and inclusive of broad genetic variability are essential to the efficient creation of superior segregates that have the adaptation(s) required by the range of environmental variations at each specific site.

Recurrent YSA and selection of genotypes over repeated seasons, followed by recurrent intercrossing among the superior genes, can create the common gene pool with the large genetic variability and adaptation that is required for the efficient generation of new and superior genotypes (Mayo 1987; Kelly and Adams 1987; Singh et al. 1989; Kenworthy and Brim 1979; Werner and Wilcox 1990). Superior combination(s) of biomass, harvest index and days to maturity with higher yield at the site will arise more frequently. Genetic diversity for other desired traits can be incorporated into the gene pool at any time through YSA-AMMI of new germ plasm and/or through crosses to exotic germ plasm having traits presumed to be beneficial to yield.

The second task of breeding

The second task of breeding (Simmonds 1989) is the selection of the most superior segregates. If only field procedures are considered, raising the efficiency of this selection is more difficult than creating larger numbers of superior segregates. Increased effort and efficiency will be required to select the best among a larger number of superior segregates. Constraint will always result due to each segregate within the early generations being a different genotype with likely segregation of its progeny. Seed quantities are small. Extensive application of YSA will not be economically feasible during the F_2 generation. However, it may be beneficial as early as the F_3 generation (Cooper 1988; Gomez 1991).

Each application of YSA-AMMI will improve our understanding of the genes and G × E that will optimize yield and of its physiological components and subcomponents for the site. YSA-AMMI will test whether a hypothesized ideotype(s) will or will not give the highest yield for that site. YSA-AMMI will detect alternative ideotype(s). With improved understanding, visual selection can become more effective. Weightings appropriate to component traits of the ideotype will become more apparent. Slowly, the second task of breeding can become more efficient. Predicted consequences can then arise from planned new combinations of traits (genes), rather than the unintended consequences that often arise when the G × E interactions and negative correlations among the components of yield are not understood and therefore cannot be considered during planning. The discarding of traits and genotypes lacking potential for high yield will be assisted.

Collaboration with biotechnologists can lead to the identification of the few maturity genes for adaptation and yield in the seed or seedling stages, rather than only after completion of whole-plant development. The use of DNA markers for the relatively few maturity genes should result in more effective selection among the segregates from crosses, i.e., more efficient fulfillment of the second task of breeding, since the maturity genes interact with the environment to jointly control the partitioning while simultaneously establishing (or failing to establish) the growth duration that adapts the genotype to that environment, plus establishing the harvest index and exerting a lesser effect on the biomass.

Interdisciplinary collaboration

The superior genotypes identified within ongoing yield trials by breeders and agronomists using YSA-AMMI can be compared in greater detail by plant physiologists, geneticists, and biochemists. YSA-AMMI can facilitate interconnected collaboration among farmers, agronomists, breeders, geneticists, physiologists, molecular biologists, etc. YSA-AMMI can also quantify genetic and environmental potentials for maximizing yield through modifying levels of fertilizer, irrigation, hormonal, or other yield-enhancing environmental factors.

Breeding for higher yield in multiple cropping systems (Smith and Francis 1986) is more difficult than breeding for yield within a sole cropping system because of competition between the crops. This competition will vary with the G × E interactions of each crop, which will vary from season to season, as will the developmental stage of each crop relative to that of the companion crop(s) and the timing of favourable and/or stress environments. YSA-AMMI of yield and its components for each crop will quantify individual-crop, inter-crop and environmental bases for the relative yields.

Even with an improved understanding of G × E interactions, their interacting complexities will continue to ensure a relatively poor judgment of the merit of a gene or trait with respect to yield. Verification of merit will require combining genes (traits) with the others and background genes with which they will interact, followed by testing for additional interaction with appropriate environment(s). Because of gene × gene and G × E interactions, even comparisons of isogenic lines are not as informative as is often implied. The rapidity of conventional breeding for yield will always be constrained by the continued segregation of genes from one early generation after a cross to the next, by a change in the interactions between major genes due to segregation of background genes, by additional changes of the gene × gene interactions due to changes of the environment, by necessity to advance the segregating progenies through multiple generations, and by necessity to test for yield plus product acceptability across multiple years (Blixt and Vose 1984; Kelly and Adams 1988; Singh et al. 1989; White and Izquierdo 1989). However, selection for yield during early segregating generations can progress toward being more effective (Blixt and Vose 1984; Mayo 1987; Singh et al. 1990) if whole-plant models for yield (the ideotype) have been correctly established for the site, to the extent that gene × gene and G × E interaction effects are understood for the site, to the extent that procedures are available for the molecular determination of presence versus absence of needed genes, and to the extent that all accessible knowledge is incorporated into selection of the parental germ plasm plus selection of the segregating and advanced generation progenies.

The first bean cross for combining high aerial biomass with high harvest index gave a genotype that accumulated the same yield as the higher-yielding parent in 15% less time. Continued recurrent selection for aerial biomass and partitioning, plus their rates, followed by recurrent intercrossing, next gave a 20% higher yield. The genotype received limited commercial acceptance because it also gave an unacceptable canned product. Current progenies are yielding 30–40% more, some with acceptable canning quality.

Improvement of site, region, and world yields

YSA-AMMI can facilitate rapid gain in yield for each production site. Yield gains at many sites will raise regional and then world yields above those that result from breeding at centralized locations with selection for broad adaptation (Anderson and Hazell 1989). Dispersal of the genetic uniformity that results in vulnerability to a common set of diseases and insects across a broad geographical region will be minimized.

Acknowledgements. Appreciation is expressed to the following collaborators. At locations broadly described within the text, the data interpreted within this paper were from yield trials conducted by some of the authors, plus by M. Brick, D. Burke, E. Cantorral, R. Gaudiel, K. Grafton, W. L. Hymes, W. H. Isom, J. Kelly, G. A. Kemp, J. Kolar, J. G. Lauer, R. Marechal, D. Nuland, C. Pearson, B. H. Rich, A. Valladolid, and D. Wood. This research is a contribution to the W-150 regional bean research project. Financial support is acknowledged from all the experiment stations, plus from the USAID funded Bean/Cowpea Collaborative Research Support Program.

References

Anderson JR, Hazell PBR (eds) (1989) Variability in grain yields: implications for agricultural research and policy in developing countries. Johns Hopkins University Press, Baltimore, Md.

Apel P (1984) Photosynthesis and assimilate partitioning in relation to plant breeding In: Vose PB, Blixt SG (eds) Crop breeding: a contemporary basis. Pergamon Press, Oxford, pp 163–184

Austin RB (1990) Prospects for genetically increasing the photosynthetic capacity of crops. In: Zelitch I, Allen NS (eds) Perspective in biochemical and genetic regulation of photosynthesis. Alan R Liss, New York, pp 395–409

Bernier G (1988) The control of floral evocation and morphogenesis. Annu Rev Plant Physiol 39:175–219

Black CC, Burris RH (eds) (1975) CO_2 Metabolism and plant productivity. University Press, Baltimore

Blixt S, Vose PB (1984) Breeding towards an ideotype – aiming at a moving target. In: Vose PB, Blixt SG (eds) Crop breeding: a contemporary basis. Pergamon Press, Oxford, pp 414–426

Blum A, Golan G, Mayer J (1991) Progress achieved by breeding open-pollinated cultivars as compared with landraces of sorghum. J Agric Sci 117:307–312

Charles-Edwards DA, Vanderlip RL (1985) interfacing the analysis and synthesis of crop growth performance. In: Day W, Atkin RL (eds) Wheat growth and modeling. Plenum Press, New York, pp 275–291

Cooper RL (1988) Breeding for yield in soybeans: early generation testing and specific adaptation to high versus low yield environments. Presented at a workshop of Centro Internacional de Agricultura Tropical, Cali, Colombia

Craufurd PQ, Bidinger FR (1988) Effect of the duration of the vegetative phase on shoot growth, development and yield in pearl millet (*Pennisetum americanum* (L.) Leeke). J Exp Bot 39:124–139

Crossa J (1990) Statistical analysis of multilocation trials. Adv Agron 44:55–85

Donald CM (1968) The breeding of crop ideotypes. Euphytica 17:385–403

Dormling I, Gustafsson A, Ekman G (1975) Growth disorders and phenotype variability in phytotron-cultivated barley. Hereditas 79:255–272

Evans LT (1983) Raising the yield potential: by selection or by design. In: Kosuge T, Meredith CP, Hollaender A (eds) Genetic engineering of plants. Plenum Press, New York, pp 371–389

Frankel OH (1947) The theory of plant breeding for yield. Heredity 1:109–120

Frey KF (1988) Increasing grain yield of oats. Plant Physiol Biochem 26:539–542

Gauch HG Jr (1988) Model selection and validation for yield trials with interaction. Biometrics 44:705–715

Gauch HG Jr (1992) Statistical analysis of regional yield trials. Elsevier, New York

Gifford RM (1986) Partitioning of photosynthate in the development of crop yield. In: Cronshaw J, Lucas WJ, Gianquinta RT (eds) Phloem transport. AR Liss, New York, pp 535–549

Gifford RM (1987) Barriers to increasing crop productivity by genetic improvement of crop yield in photosynthesis. In: Biggins J (ed) Progress in photosynthesis. Martinus Nijhoff, Dordrecht, The Netherlands, vol. IV, pp 377–384

Gniffke PA (1985) Studies of phenological variation in the common bean (*Phaseolus vulgaris* L.) as modulated by mean temperature and photoperiod. PhD thesis, Cornell University, Ithaca, N.Y.

Gomez H (1991) Early generation selection of beans (*Phaseolus vulgaris* L.) under wide environmental variation. PhD thesis, Cornell University, Ithaca, N.Y.

Harper JE, Schrader LE, Howell RW (1985) Exploitation of physiological and genetic variability to enhance crop productivity. Am Soc Plant Physiol, Rockville Md.

Hayashi K (1969) Efficiencies of solar energy conversion in rice varieties as affected by cultivating period. Crop Sci Soc Jpn 38:528–533

Hodges T (1991) Predicting crop phenology. CRC Press, Boca Raton, Fla.

Hoogendoorn J (1985) The physiology of variation in the time of ear emergence among wheat varieties from different regions of the world. Euphytica 34:559–571

Jordan DB, Ogren WL (1983) Species variation in kinetic properties of ribulose 1,5-bisphospate carboxylase-oxygenase. Arch Biochem Biophys 227:425–433

Kang MS (1990) Understanding and utilization of genotype-by-environment in plant breeding. In: Kang MS (ed) Genotype by environment interaction and plant breeding. Louisiana State University, Baton Rouge, La., pp 126–140

Kelly JD, Adams MW (1987) Phenotypic recurrent selection in ideotype breeding of pinto beans. Euphytica 36:69–80

Kenworthy WJ, Brim CA (1979) Recurrent selection in soybeans. I. Seed yield. Crop Sci 19:315–318

Kinet JM, Sachs RM, Bernier G (1985) The physiology of flowering, vol. III. CRC Press, Boca Raton, Fla.

Lambers H, Cambridge ML, Konings H, Pons TL (1990) Causes and consequences of variations in growth rate and productivity of higher plants. SPB Academic Publishing, The Hague

Lawn RR (1990) Agronomic and physiological constraints to the productivity of tropical grain legumes and prospects for improvement. Exp Agric 25:509–528

Mahon JD (1990) Photosynthesis and crop productivity. In: Zelitch I, Allen NS (eds) Perspectives in biochemical and genetic regulation of photosynthesis. Alan R Liss, New York, pp 379–394

Masaya PN, White JF (1991) Adaptation to photoperiod and temperature. In: van Schoonhoven A, Voysest O (eds) Common beans: research for crop improvement. CAB International, Wallingford, UK, pp 445–500

Mayo O (1987) The theory of plant breeding, 2nd edn. Clarendon Press, Oxford

Myers JR (1988) Thirty-nineth Annual Report of the Cooperative Dry Bean Nurseries. University of Idaho, Kimberly, Idaho

Murfet IC (1977) Environmental interaction and the genetics of flowering. Annu Rev Plant Physiology 28:253–278

Rasmusson DC (1987) An evaluation of ideotype breeding. Crop Sci 27:1140–1146

Robertson LD, Frey KJ (1987) Honeycomb design for selection among homozygous oat lines. Crop Sci 27:1105–1108

Ross JJ, Murfet IC (1985) A comparison of the flowering and branching control systems in *Lathyrus odoratus* L and *Pisum sativum* L. Ann Bot 56:847–857

Russell RS (1977) Plant root systems: their function and interaction with the soil. McGraw-Hill, New York

Salisbury FB, Ross CW (1991) Plant physiology, 4th edn. Wadsworth Publ, Belmont, Calif.

Scully BT, Wallace DH (1990) Variation in and relationship of biomass, growth rate, harvest index, and phenology to yield of common bean. J Am Soc Hortic Sci 115:218–225

Scully BT, Wallace DH (1991) Heritability and correlation of biomass, growth rates, harvest index, and phenology to the yield of common beans. J Am Soc Hortic Sci 116:127–130

Sedgley RH (1991) An assessment of the Donald ideotype after 21 years. Field Crops Res 26:93–112

Simmonds NW (1989) How frequent are superior genotypes in plant breeding populations. Biol Rev 64:341–365

Singh SP, Cajiao C, Gutierrez JA, Garcia J, Pastor-Corralles MA, Morales FJ (1989) Selection for seed yield in inter-gene pool crosses of common bean. Crop Sci 29:1126–1131

Singh SP, Lepiz R, Gutierrez JA, Urrea C, Molina A, Teran H (1990) Yield testing of early generation populations of common bean. Crop Sci 30:874–878

Smith ML, Francis CA (1986). Breeding for multiple cropping systems. In: Francis CA (ed) Multiple cropping systems. Macmillan Publ, London, pp 219–249

Snyder FW, Carlson GE (1984) Selecting for partitioning of photosynthetic products in crops. Adv Agron 36:47–72

Squire GR (1990) The physiology of tropical crop production. Bookcraft, Bath, UK

Summerfield RD, Roberts EH (1988) Photo-thermal regulation of flowering in pea, lentil, faba bean and chickpea. In: World crops: cool season legumes. Kluwer Academic Publ, Norwell, Mass., pp 911–922

Syme JR (1973) Quantitative control of flowering time in wheat cultivars by vernalization and photoperiod sensitivities. Aust J Agric Res 24:657–665

Takeda K, Frey KJ (1987) Improving grain yield in backcross populations from *Avena sativa* × *A. sterilis* matings by using independent culling for harvest index and vegetative growth index or unit straw weight. Theor Appl Genet 74: 659–665

Tollenaar M (1991) Physiological basis of genetic improvement of maize hybrids in Ontario from 1959 to 1988. Crop Sci 31:119–124

Tollenaar M, Hunter RB (1983) A photoperiod and temperature sensitive period for leaf number of maize. Crop Sci 23:457–460

Torigoe Y (1986) A conceptual model of developmental phases of maize on the basis of the relationship between differentiation and growth of vegetative and reproductive organs. Jpn J Crop Sci 55:465–473

Vince-Prue D (1975) Photoperiodism in plants. McGraw Hill, New York

Vince-Prue D, Thomas B, Cockshull KE (eds) (1984) Light and the flowering process. Academic Press, London

Wallace DH (1973) Commentry upon: Plant architecture and physiological efficiency in the field bean. In: Seminar on potentials of field beans and other food legumes in Latin America. Series Seminar No. 2E. Centro Internacional de Agricultura Tropical, Cali, Colombia

Wallace DH (1980) The genetics of photosynthesis and crop productivity with emphasis on beans. In: (eds) Well-being of mankind and genetics vol. 1 book 2. Proc XIV Int Congr Genet. MIR Publ, Moscow, pp 306–317

Wallace DH (1985) Physiological-genetics of plant maturity, adaptation and yield. Plant Breeding Reviews 3:21–167

Wallace DH (1991) System analysis of yield trials can raise efficiency of breeding for yield. In: Prakash J, Peirik RLM (eds) Proc Int Seminar New Frontiers Hortic. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 1–10

Wallace DH, Enriquez GA (1980) Daylength and temperature effects on days to flowering of early and late maturing beans (*Phaseolus vulgaris.* L). J Am Soc Hortic Sci:105–583–591

Wallace DH, Masaya PN (1988) Using yield trial data to analyze the physiological genetics of yield accumulation and the genotype × environment interaction effect on yield. Annu Rep Bean Improvement Coop 31:vii–xxiv

Wallace DH, Zobel RW (1982) The biology of crop yield. In: Rechcigl M Jr (ed) Handbook of crop productivity. CRC Press, Boca Raton, Fla., pp 137–142

Wallace DH, Peet MM, Ozbun JL (1976) Studies of CO_2 metabolism in *Phaseolus vulgaris* L. and applications in breeding. In: Burris RH, Black CC (eds) CO_2 metabolism and plant productivity. University Press, Baltimore, pp 43–58

Wallace DH, Gniffke PA, Masaya PN, Zobel RW (1991) Photoperiod, temperature and genotype interaction effects on days and node to flower of bean (*Phaseolus vulgaris* L.) J Am Soc Hortic Sci 116:534–543

Wallace DH, Yourstone KS, Masaya PN, Zobel RW (1993a) Photoperiod gene control over partitioning between reproductive and vegetative growth. Theor Appl Genet 86:6–16

Wallace DH, Zobel RW, Yourstone KS (1993c) A whole-system reconsideration of paradigms about photoperiod and temperature control of crop yield. Theor Appl Genet 86: 17–26

Wardlaw IF (1990) The review of carbon partitioning in plants. New Phytol 116:341–381

Werner BK, Wilcox JR (1990) Recurrent selection for yield in *Glycine max* using male sterility. Euphytica 50:19–25

Whisler FD, Acock B, Baker DN, Fye RE, Hodges HF, Lambert JR, Lemmon HE, McKinion JM, Reddy VR (1986) Crop simulation models in agronomic systems. Adv Agron 40:141–208

White JW, Izquierdo J (1989) Dry bean: physiology of yield potential and stress tolerance. Centro Internacional de Agricultura Tropical, Cali, Colombia, and FAO Regional Office for Latin America and the Caribbean. Santiago, Chile

Wolf S, Marani A, Rudich J (1990) Effects of temperature and photoperiod on assimilate partitioning in potato. Ann Bot 66:513–520

Yourstone KS (1988) Photoperiod and temperature interaction effects on time to flower and its components in bean (*Phaseolus vulgaris* L.). PhD thesis, Cornell University, Ithaca, N.Y.

Yourstone KS, Wallace DH (1990) Effects of photoperiod and temperature on rate of node development in indeterminate bean. J Am Soc Hortic Sci 115:824–828

Zelitch I (1971) Photosynthesis, photorespiration and plant productivity. Academic Press, New York

Zobel RW (1990) A powerful statistical model for understanding genotype-by environment interaction. In: Kang MS (ed) Genotype by environment interaction and plant breeding. Louisiana State University, Baton Rouge, La., pp 126–140

Zobel RW, Wright MJ, Gauch HG (1988) Statistical analysis of a yield trial. Agron J 80:388–393