Improving efficiency of breeding for higher crop yield

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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
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 x 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 x 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...