

Chapter 3

Physiology of Growth and Yield Components

INTRODUCTION

Crop yield is determined by plant growth and partitioning of biomass to marketable parts of plants. Both growth and partitioning are affected by developmental stages of crops. Knowledge of physiological processes of growth, development, and partitioning into yield components is necessary for a basic understanding of maximizing crop yield. It is important first to define growth.

Growth refers to biomass accumulation and can be measured by leaf area, shoot, root, and total weights, or plant height, and these can be used to compare within cultivars or between cultivar means (McCauley, 1990). The term growth also applies to quantitative changes that occur during development and may be defined as an irreversible change in the size of cells, organs, or whole organisms (Wareing and Phillips, 1981). Wilhelm and McMaster (1995) defined growth simply as irreversible increases in physical dimension of individuals or organs with time. Therefore, examples of growth are irreversible lengthening of leaf blade tissue or increases in leaf area. In agriculture, where the purpose of most enterprises is to convert solar energy into dry matter, an equally useful definition of growth is increased dry weight. Growth is affected by environmental factors such as climate, soil, and plants themselves. Growth is sometimes confused with development. These two terms are interrelated but different.

Plant development may be defined as the sequence of ontogenetic events, involving both growth and differentiation, leading to changes in function and morphology (Landsberg, 1977). Development is generally measured over time between various physiological stages. Development includes processes of organ initiation (morphogenesis)

but extends to differentiation and ultimately includes processes of senescence. The process by which plants, organs, or cells pass through various identifiable stages during their life cycles can be considered a functional definition of development. Phyllochrons (interval between similar growth stages of successive leaves on the same culm) have been used extensively to describe and understand development of grasses (Wilhelm and McMaster, 1995). Development may be affected slightly by factors influencing growth but is more closely related to heat unit accumulation (Stansel, 1975). Growth and development in crop plants do not proceed at constant or fixed rates through time. They are modified by environmental factors such as temperature, light intensity and duration, nutrition, and cultural practices. Therefore, calendar date is not suitable as quantitative descriptions for developmental stages of plants. Many attempts have been made to define precise and easily applicable methods for describing each important period and stage during cereal development. The scales used to assess development of cereals have been described by Landes and Porter (1989). These authors identified 23 scales, which are separated into those that codify external development of plants and those that describe events at apical meristems. Similarly, growth stages of legumes such as soybean and common bean have also been described (Fageria, 1992).

THEORY OF GROWTH AND YIELD COMPONENTS ANALYSIS

Techniques used to quantify components of crop growth are collectively known as growth analysis. Growth analysis techniques have made substantial contributions to current concepts of crop yield physiology. Functional growth analysis, based on experiments in which plants are grown under standard conditions and harvested at regular intervals, can provide the first clues toward an understanding of variation in growth rates among genotypes or species (Lambers, 1987). Plant growth analysis can also be used to evaluate effects of cultural management practices such as fertilization, plant spacing and density, irrigation treatments, and disease, insect, and weed control. Plant growth analysis, demographic analysis, and yield component analysis are three procedures used to study relationships associated with plant growth and development (Jolliffe, Eaton, and Doust, 1982).

Plant growth analysis is generally expressed as indexes of growth such as crop growth rate, relative growth rate, net assimilation rate, leaf area ratio, and leaf area index. Discussion of these growth indexes follows.

Crop Growth Rate

Dry matter accumulation rate per unit land area is referred to as crop growth rate (CGR). It has been calculated as follows:

$$\text{CGR} = (W_2 - W_1) / SA (t_2 - t_1) \quad (3.1)$$

where CGR is crop growth rate expressed in $\text{g}\cdot\text{m}^{-2}$ per day or $\text{kg}\cdot\text{ha}^{-1}$ per day, W_1 and W_2 are crop dry weights at the beginning and end of intervals, t_1 and t_2 are corresponding days, and SA is the land area occupied by plants at each sampling. Crop growth patterns can be defined accurately by taking plant samples at different time intervals during the growing season. Values of CGR are normally low during early growth stages and increase with time, reaching maximum values at about the time of flowering. Analysis of CGR is important for evaluating treatment differences among crop species or cultivars within species in relation to yield. Some CGR values of some important annual crops are presented in Table 3.1. Lowland rice had maximum CGR values and common bean had minimum.

Relative Growth Rate

Relative growth rates (RGR) of plants at specific instants in time (t) are defined as increases in plant dry matter per unit plant material per unit time (Radford, 1967). These RGR values can be calculated using the following formula and are expressed as gram per gram dry weight per day ($\text{g}\cdot\text{g}^{-1}$ dry wt. per day) or $\text{kg}\cdot\text{ha}^{-1}$ dry wt. per day.

$$\text{RGR} = (1/W) \times (dW/dt) = (d/dt) (\log_e W) \quad (3.2)$$

where W is the dry weight and dW/dt is the change in dry weight per unit time. Values of RGR are generally higher during early growth stages of crop growth and decrease with advancement in age. Curves

TABLE 3.1. Maximum growth rates during growth cycles of upland and lowland rice, common bean, maize, and soybean grown on an Oxisol and Inceptisol in central Brazil.

Crop species ^a	CGR (kg-ha ⁻¹ /day)
Upland rice (90-99 days after sowing)	229
Lowland rice (98-111 days after sowing)	385
Common bean (43-62 days after sowing)	66
Maize (35-53 days after sowing)	311
Soybean (102-120 days after sowing)	138

Source: Fageria, 1998.

^aLowland rice was grown on an Inceptisol and the other crops were grown on an Oxisol. Growth cycle of upland rice was 130 days; lowland rice was 141 days; common bean was 96 days; maize was 119 days; and soybean was 158 days.

for RGR of crops are opposite to dry matter accumulation during life cycles of crops.

Net Assimilation Rate

Dry matter accumulation per unit of leaf area is termed net assimilation rate (NAR) and is expressed as grams per square meter of leaf area per day (g-m⁻² leaf area/day), and can be calculated using the following formula (Brown, 1984):

$$\text{NAR} = (1/A) (dW/dt) \quad (3.3)$$

where A is leaf area and dW/dt is the change in plant dry matter per unit time. The objective of measuring NAR is to determine efficiency of plant leaves for dry matter production. NAR values decrease with crop growth due to mutual shading of leaves and reduced photosynthetic efficiency of older leaves (Fageria, 1992).

Leaf Area Ratio

Leaf area ratios (LAR) of plants at specific instants in time (t) are defined as ratios of assimilatory plant material per unit of plant material. This growth parameter is calculated as follows:

$$\text{LAR} = (A/W) \quad (3.4)$$

where A is leaf area and W is plant dry weight.

Leaf Area Index

Leaf area index (LAI) is defined as leaf area per unit soil area ($\text{cm}^2\text{-m}^{-2}$). This growth index can be calculated as follows (Watson, 1958):

$$\text{LAI} = (A \times N)/10,000 \quad (3.5)$$

where A is leaf area (cm^2) and N is number of tillers (cereals), branches (legumes), or plants per m^2 .

Watson (1958) pointed out that crop growth rates (CGR) could be calculated from LAI and NAR as follows:

$$\text{CGR} = \text{LAI} \times \text{NAR} \quad (3.6)$$

Demographic Analysis

Bazzaz and Harper (1977) first applied demographic analysis to study plant growth. Demography follows births and deaths of individual components, and demographic analyses study dynamics of leaf populations and flower populations (Abul-Faith and Bazzaz, 1980). Hunt (1978) pointed out that demography can be used in addition to traditional plant growth analysis.

YIELD COMPONENTS ANALYSIS

Yield components analysis subdivides plant development into stages of growth. Indexes called yield components represent those stages of growth, and plant yield or productivity is the mathematical value of yield components (Jolliffe, Eaton, and Doust, 1982). Hardwick (1976) studied origins of yield components analysis to improve agricultural productivity. For example, yield components analysis provided key physiological information during the selection of some modern high-yielding rice cultivars (Yoshida, 1972). The interpretation of quantitative relationships among yield components has been advanced in

recent years through the use of correlation analysis and partial regression analysis. Yield components are important in many crop research programs. Plant breeders often seek to improve yield by selecting components of yield such as seeds per plant or thousand-kernel weight. A complex character of yield may be defined as a character for which variation is determined by variations in numbers of component traits (Bos and Sparnaaij, 1993; Piepho, 1995). Perry and D'Antuono (1989) concluded that 80 percent of overall increases of some Australian spring wheat cultivar yields were due to increased harvest index values. Grains per ear and grains per m^2 were strongly and positively correlated with grain yield, but weak negative correlations were noted between 1000-grain weight and yield. Cultivars with semi-dwarf backgrounds had equal biomass, but higher yields, harvest index values, ear numbers per m^2 , and grains as compared to modern tall cultivars. Perry and D'Antuono (1989) also concluded that genetic improvement substantially increased yield potentials of wheat, which was achieved through substantial increases in grain numbers per m^2 and with improved harvest indexes. Mean harvest indexes were 0.29 for older wheat cultivars and 0.36 for more recent semi-dwarf cultivars.

Among components for grain yield of cereal crops, numbers of spikelets appear to be important in developing high-yielding cultivars (Feil, 1992). However, increasing numbers of spikelets per panicle in rice may cause overproduction of spikelets on secondary branches (Yamamoto et al., 1991). In contrast to spikelets on primary branches, grain spikelets on secondary branches generally do not fill sufficiently (Kato, 1993). Thus, increasing numbers of spikelets per panicle does not always result in higher yields. Breeders frequently face conflicting requirements for improving yield, that is, increasing both numbers of spikelets per panicle as well as filled grain percentages (Kato, 1997).

Grain yield in field crops is determined by various yield components. Important yield components in cereals are panicles or ear per unit area, numbers of spikelets per panicle or ear, and spikelet weights. Similarly, yield components in legumes are determined by numbers of pods per unit area, grains per pod, and dry weights of grain. In cereals, relationships between yield and yield components can be expressed as follows (Fageria, 1992):

$$\begin{aligned}
 \text{Grain yield} &= \text{numbers of panicles or ears m}^{-2} \\
 &\times \text{numbers of spikelets per panicle or ear} \\
 &\times 1,000 \text{ grain weight (g)} \\
 &\times \text{filled spikelets (percent)} \times 10^{-5} \qquad (3.7)
 \end{aligned}$$

For example, to obtain a rice crop of 6 t·ha⁻¹ grain yield, it would be necessary to have a combination of the following yield-attributing characters or components:

1. 400 panicles per m²,
2. 80 spikelets per panicle,
3. 85 percent filled spikelets, and
4. 22 g weight 1,000 grains.

By putting these values into the above equation,

$$\text{Grain yield} = 400 \times 80 \times 0.85 \times 22 \times 10^{-5} = 6 \text{ t}\cdot\text{ha}^{-1}. \quad (3.8)$$

This yield equation is based on the fact that combinations of grain numbers, grain weights, and spikelet numbers are essential to raise yield levels in most grain crops. Several studies have shown that these components are negatively correlated and difficult to combine (Sinha and Swaminathan, 1984). Nevertheless, we know that despite having negative correlations, yields have been improved in many crops, especially for wheat and rice. An understanding of these crop development properties can be useful in breaking these correlations. Appropriate agronomic practices such as seeding rates to obtain optimum numbers of spikelets per unit area can also help offset negative correlations observed.

Among yield components, numbers of panicles have usually been the most variable for rice even though it has been related to grain yield (Figures 3.1 and 3.2). Grain yield increased quadratically with increasing numbers of panicles, and maximum yield was achieved at about 583 panicles per m² (calculated from regression analysis). Varying plant density and tillering performance can vary numbers of panicles per unit area.

Other yield components have also been associated with crop yield, but many have not. For example, harvest index (grain yield/grain plus

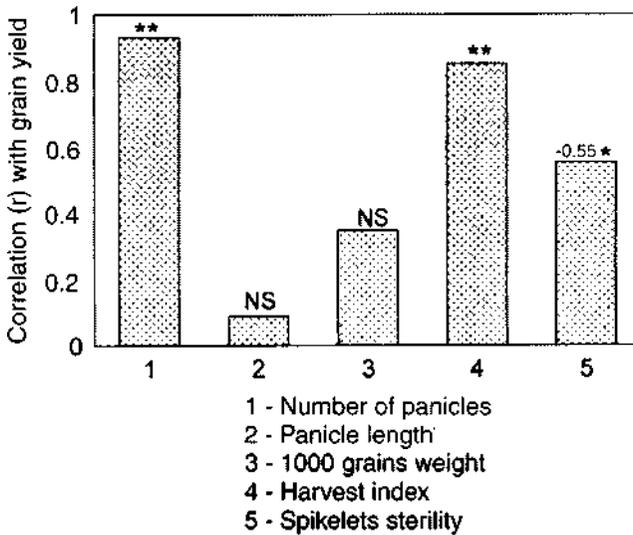


FIGURE 3.1. Correlation between grain yields and yield components of lowland rice. *Source:* Reproduced from Fageria, 1998.

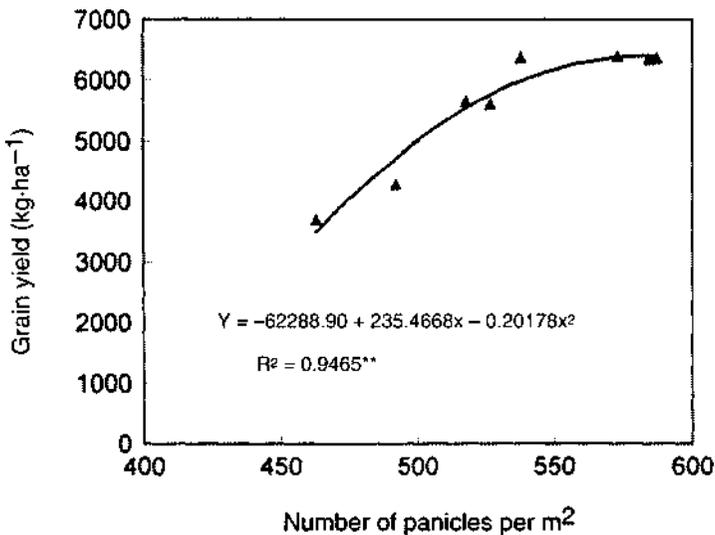


FIGURE 3.2. Relationship between numbers of panicles and grain yield of lowland rice. *Source:* Reproduced from Fageria, 1998.

straw yield) has been positively correlated with grain yield, but spikelet sterility has been negatively correlated. Beyond certain plant densities, negative correlations exist between components of yield capacity so that yields tend to become constant under given sets of conditions. Such correlations appear to be developmental rather than genetic (Yoshida, 1972). Dofing and Knight (1994) evaluated performance and yield component contributions for yield of five unicultm barley genotypes. Results from path analysis demonstrated that spikes per square meter was the primary determinant of grain yield, followed by kernels per spike, with kernel weight of only minor importance. Increasing spikelets per square meter caused relatively large reductions in kernels per spikelet and kernel weights, while increasing kernels per spikelet caused only minor reductions in kernel weights.

Yield components do not influence crop yields independently but are closely related to one another. In many cases, increases of one component cause declines of other components. For example, increased numbers of panicles were associated with decreased numbers of grains per panicle. It has also been a general tendency that increases in number of grains per unit area cause decreases in percentage of ripened grains (Matsushima, 1976). This means it is possible to increase yield components independently with some management practices, but grain yields generally have not increased as expected.

Examples of using the yield equation for grain yields of legumes are given as follows:

$$\text{Yield (t}\cdot\text{ha}^{-1}) = \text{pod number m}^{-2} \times \text{grain number per pod} \\ \times 1,000 \text{ grain weight (g)} \times 10^{-5} \quad (3.9)$$

or

$$\text{grain number m}^{-2} \times 1,000 \text{ grain weight (g)} \times 10^{-5} \quad (3.10)$$

To obtain yields of 1.5 t·ha⁻¹ cowpea, the following combination of yield components would be needed: 155 pods per m², seven grains per pod, and 140 g for 1,000 grains. By putting these values into the above equation, the result would be

$$\text{Grain yield} = 155 \times 7 \times 140 \times 10^{-5} = 1.5 \text{ t}\cdot\text{ha}^{-1} \quad (3.11)$$

In addition, Akhter and Sneller (1996) used the following yield component model to determine soybean grain yields:

$$\begin{aligned} \text{Plot yield} = & \text{plants per plot} \times [(\text{main stem nodes/plant} \\ & \times \text{pods/node} \times \text{seeds/pod} \times \text{grams/seed}) \\ & + (\text{branches/plant} \times \text{pods/branch} \\ & \times \text{seeds/pod} \times \text{grams/seed})] \end{aligned} \quad (3.12)$$

Numbers of main stem nodes, main stem pods, branches, pods on branches, and seeds were counted for each plant. Pods per main stem node were calculated by dividing numbers of pods on main stems by numbers of main stem nodes. Numbers of pods per branch were calculated by dividing total numbers of pods on branches by numbers of branches. Numbers of seeds per pod for main stems and branches were calculated by dividing total numbers of seeds per plant by total numbers of pods per plant. Seed weights were determined by dividing total weights of seeds per plant by numbers of seeds per plant. These yield components could be classified into primary yield components affecting final yield (seed numbers and seed sizes), secondary yield components affecting seed numbers (seeds per pod and pod numbers), and tertiary yield components affecting pod numbers (reproductive node numbers, pods per reproductive node, percent nodes being reproductive, and node numbers).

Greater understanding of how yield components influence yield formation on phenotypic and genotypic levels can be obtained by applying path analyses to determine direct and indirect effects of primary, secondary, and tertiary yield components on their respective response variables (yield, seed numbers, and pod numbers, respectively). Such analyses will help clarify which yield components are most important for mediating environmental (especially crop growth rate and light interception) and genetic effects on yield (Board, Kang, and Harville, 1999).

Analysis of 12 soybean cultivars grown in narrow and wide row spacing revealed that yield was positively correlated with pod numbers and total dry matter at the R_5 growth stage, but not seeds per pod or seed size (Board, Zhang, and Harville, 1996). These results led to speculation that genetic improvements of late-planted soybean yields may result from selection for pod numbers or yield components influencing pod numbers. Because pod numbers are largely determined by

crop growth rates during emergence to the R_5 growth stage (Board, Kamal, and Harville, 1992), genetic differences in pod numbers could be caused by genetic differences in crop growth rate. However, path analysis revealed that seed or pod numbers are poor predictors for genetic effects on yield (Board, Kang, and Harville, 1999).

Number of pods in legumes such as soybeans has been a critical yield component trait (Fageria, Baligar, and Jones, 1997) even though some cultivars known to initiate large numbers of pods did not produce high yields. In fact, shedding of growing pods, shell enlargement, seed abortion, or nonoptimal seed growth may contribute to reductions of yield potential. Environmental stresses due to high temperature (Egli and Wardlaw, 1980) and water deficits (Meckel et al., 1984) may cause pod and seed losses. Thus, it is important to simulate the dynamics of pod and seed setting and to specify effects of genetic and climate factors on each yield component (Colson, Bouniols, and Jones, 1995). For example, Board, Kang, and Harville (1999) reported that although several yield components of soybean were being formed simultaneously, changes in source strength affected some traits. That is, rapid seed filling commenced near the R_6 growth stage, and seed growth rate commenced during rapid seed filling and was influenced by numbers of cotyledonary cells, which formed between the R_3 (Peterson et al., 1992) and R_6 (Egli, 1994) stages of growth. Other studies indicated that changes in assimilatory capacity during this period of growth could reduce cotyledonary cell numbers, resulting in slower seed growth rates and decreased seed size (Guldan and Brun, 1985). Seeds per pod are determined starting from shortly after the R_1 (Peterson et al., 1992) to near the R_6 growth periods when pod extension is completed (Pigeaire, Duthion, and Turc, 1986). Major factors affecting pod numbers (pods per reproductive node and reproductive node numbers) are also determined during the R_1 to R_6 growth periods (Board and Tan, 1995). Board, Kang, and Harville (1999) concluded that the best genetic approach to improve yield at late plantings of soybeans is to select for cultivars or genotypes with high pods per reproductive node but which at the same time do not show compensatory interactions between seed numbers and seed size.

Higher crop yields are achieved only when appropriate combinations of yield component traits occur. Similarly, higher dry matter yields are related to higher grain yields. Understanding the physiology

of dry matter production and yield component traits can help in manipulation of these yield-determining factors to favor higher yields.

DRY MATTER PRODUCTION AND GRAIN YIELD

Dry matter does not mean any single substance but refers to the entire organic dry matter that is produced from essential activities of photosynthesis and protein metabolism. Organic dry matter includes glucose, starch, cellulose, amino acids, protein, and other organic components (Akita, 1995). Dry matter of plants refers to total biological yield which includes leaves, stalks, straw, roots, and other plant parts that may not be used commercially as well as economically useful parts such as grains, tubers, and fruits. For agricultural purposes, dry matter yields of many crops refer to aboveground (soil) grown plant parts but may contain belowground plant parts for some crops such as potatoes, yams, taro, cassava, and some vegetable crops. Whole-plant aboveground biomass is the economically useful part of forage plants, while grain is the main useful part of cereals and soybeans. For cereals and legumes, grain yields are related to total biomass yields as well as other yield component traits. For example, grain yield of cereals and soybeans has been related to harvest index as follows (Donald and Hamblin, 1976):

$$\begin{aligned} \text{Grain yield} &= \text{biological yield (straw + grain)} \\ &\times \text{harvest index} \end{aligned} \quad (3.13)$$

According to the above equation, crop production can be measured as total biomass or economically useful plant parts. Total yield of plant material is known as biological yield, and ratio of grain yield to biological yield is harvest index (Huhn, 1990). Grain yields correlated positively with biological yields of pigeon pea, mung bean, and urd bean (Snyder and Carlson, 1984). These authors concluded that biological yield did not seem to be related to limited high grain yield, but harvest index was related to limited yield of these three plant species. Therefore, greater emphasis could be placed on breeding for high harvest indexes for cultivars of these plant species.

Efficiency of grain production in crop plants has also been frequently related to harvest index. Sinclair (1998) and Hay (1995) stated that harvest index is an important trait associated with the

dramatic increases in crop yields during the twentieth century. Harvest index reflects partitioning of photosynthate between grain and vegetative plant parts. Improvements in harvest index emphasize the importance of C allocation in grain production. By definition, harvest index values are <1 , but some researchers prefer to express values as percentages.

Grain yield has also been related directly to harvest index even though biological yield and harvest index may not be related. Snyder and Carlson (1984) reviewed relationships of harvest index to yield and reported that harvest index correlated positively with grain yield and negatively with biological yield of barley, oats, rye, wheat, soybean, pigeon pea, and mung bean. Thus, selecting for higher harvest indexes should increase grain yield in most cases, particularly when biological yield is relatively stable. Increased harvest indexes have contributed to increasing yields of rice, barley, and wheat; values of more than 50 percent have been achieved for these cereals. However, limits of how far harvest index values can be improved is unknown. It appears that these values will not be able to rise much above 60 percent in cereals, although they may go further in root and tuber crops (Evans, 1980). Further increases in yield potential will depend on improvements in rates of photosynthesis and growth. Increases in harvest index of maize have been modest (from 45 percent in the 1930s to 50 percent in the 1980s), and much of maize yield increases have resulted from increases in total crop mass (Russell, 1985). Accumulation of high levels of N is essential for high maize grain yields, and high levels of N are commonly associated with crops having high harvest indexes (Sinclair, 1998). Under conditions where N has been limited, low harvest indexes of crops have been advantageous. Limited N can be partitioned into vegetative tissue of low N concentration, which results in higher total production of plant mass than in tissues of high N concentration. However, increasing grain yield and crop harvest index with high N grain requires concomitant increases in crop N accumulation (Sinclair, 1998).

Ranges in harvest index values among crop plants are considerable. Snyder and Carlson (1984) noted that harvest index for a semi-dwarf wheat was 47 percent, compared to 40 percent for standard cultivars, and varied from 23 to 50 percent for 21 late-duration, high-yielding rice cultivars. Harvest index values for peanut ranged from 20 to 47 percent for bunch types, 3 to 31 percent for semi-spreading

types, and 10 to 22 percent for spreading types. Harvest index values for 23 cultivars of common bean varied from 39 to 58 percent. Snyder and Carlson (1984) also reported a cassava cultivar (M Col 22) at nine months of age having 80 percent of its total weight in root material. This has been one of the highest percentages of economic yield reported for any root crop. These large genetically controlled ranges in harvest indexes among various crops, coupled with significant correlations between harvest index and economic yield, have contributed to plant breeder success for using harvest index as a selection criterion to increase economic yields of crops (Snyder and Carlson, 1984). For several important crop species, harvest indexes (Table 3.2) and biological yield and economic yield based on glucose (Table 3.3) have been reported.

TABLE 3.2. Harvest index (percent) of five cereal crops.

Crop	Minimum	Maximum	Average
Millet	16	40	26
Sorghum	25	56	27
Maize	25	56	42
Rice	34	55	44
Wheat	35	49	41

Source: Van Duivenbooden, De Wit, and Van Keulen, 1996; Fageria, Baligar, and Jones, 1997.

TABLE 3.3. Biological and economic yield and harvest indexes of some important field crops.

Crop	Biological yield (g CH ₂ O·m ⁻²)	Economic yield (g CH ₂ O·m ⁻²)	Harvest index
Rice	1324	657	0.50
Wheat	1957	1125	0.57
Maize	2240	1157	0.52
Soybean	816	392	0.49
Sugar beet	2174	1436	0.66

Source: Adapted from Osaki, Fujisaki et al., 1993.

Differences in translocation of photosynthate to grain may account for differences in harvest indexes (Gent and Kiyomoto, 1989). The ability of plants to retain and efficiently remobilize photosynthate to grain through maturity may also influence harvest index and yield. Almost half of plant photosynthate before anthesis is lost from wheat plants at maturity (Austin et al., 1977), and similar fractions may be lost during grain filling. Photosynthate is lost by respiration and by abscission of plant material during senescence. Wheat plants that efficiently remobilize photosynthate to grain during maturation may retain more photosynthate and provide higher harvest indexes (Gent and Kiyomoto, 1989).

Plants with any combination of morphophysiological traits that offer high harvest indexes and high grain yield deserve consideration in plant breeding programs. Limits to which harvest index can be increased are considered to be around 60 percent (Austin et al., 1980). Hence, cultivars with low harvest indexes would indicate that further improvements in partitioning of biomass are likely. On the other hand, cultivars with harvest indexes between 50 and 60 percent would probably not be improved further (Sharma and Smith, 1986).

Harvest index has been shown to be positively related to grain yield in wheat (Kulshrestha and Jain, 1982; Singh and Stoskopf, 1971). Donald and Hamblin (1976) suggested that plant breeders should use biomass and harvest index traits as early-generation selection criteria. Harvest indexes along with grain yields have been selection criteria for improving yields of cereals by several researchers (Austin et al., 1980; Riggs et al., 1981; Sedgley, 1991; Peng et al., 2000).

It was noted that 72 percent of grain yield variability in field studies of 49 spring wheat cultivars were associated with harvest index values from single plants grown under greenhouse conditions (Syme, 1972). Indirect selection for oat grain yields using harvest index was 43 percent as efficient as direct selection (Rosielle and Frey, 1975). Harvest indexes of spaced plants were superior to grain yields for prediction of wheat grain yields in large field plots (Fischer and Kertesz, 1976). Bhatt (1977) reported that harvest index was a useful selection criterion for improving grain yields of two wheat crosses in segregating generations. Harvest index was found to have merit as a selection criterion for grain yields in two crosses of spring wheat and

was considered more reliable at high plant populations than at low population densities (Nass, 1980).

Genetic improvement in yield potentials of many crops has resulted from increases in harvest indexes (Austin et al., 1980; Riggs et al., 1981; Peng et al., 2000), which have been associated with ideotypic characters such as short stature in wheat and uniculms in maize and sunflower (Sedgley, 1991). However, many researchers have also reported improvement in yield potentials of many crops to be associated with increased biomass yields in wheat (Waddington et al., 1986), maize (Tollenaar, 1989), and soybean (Cregan and Yallich, 1986). Improvements in grain yields have been related to both dry matter accumulation and harvest indexes in wheat, barley, and oat (McEwan and Cross, 1979; Wych and Rasmusson, 1983; Wych and Stuthman, 1983). Peng et al. (2000) reported that increasing trends for yields for rice cultivars released before 1980 were mainly due to improvements in harvest indexes, while increases in total biomass were associated with yield trends for cultivars released after 1980. Hybrid rice had about 15 percent higher yields than inbreds mainly because of increases in biomass production rather than in harvest indexes (Song, Agata, and Kawamitsu, 1990; Yamauchi, 1994). This would indicate that further improvement in rice yield potentials might come from increased biomass production rather than increased harvest indexes.

Grain yields are related to dry matter production as well as harvest indexes (Fageria, 1992). Leaf area index is one of the most important plant growth indexes for determining dry matter yields, and consequently yield. Increasing LAI values increases dry matter production. Obtaining improved or optimum LAI values for plant species or cultivars within species may become advantageous traits to use in plant breeding programs.

Dry matter production at different growth stages for lowland and upland rice grown on an Inceptisol and Oxisol in central Brazil is presented in Figures 3.3 and 3.4. In the case of lowland rice (Figure 3.3), vegetative dry matter increased relatively slowly during the first 40 to 50 days but increased greatly from 50 to 120 days. Increases in dry matter during growth of this plant were attributed mainly to high photosynthesis from increased leaf area (Fageria, Santos, and Baligar 1997). Vegetative dry matter decreased 24 percent during grain filling, as active translocation of assimilates occurred from leaves/stalks

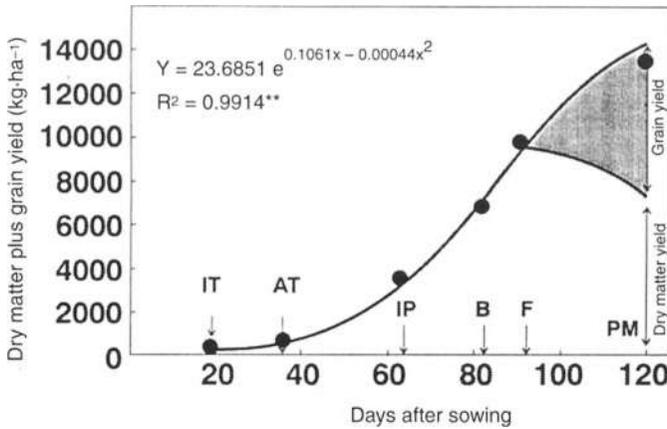


FIGURE 3.3. Dry matter accumulation and grain yield of lowland rice grown in central Brazil on an Inceptisol. *Source:* Reproduced from Fageria, 1998. *Note:* IT = initiation of tillering; AT = active tillering; IP = initiation of panicle; B = booting; F = flowering; and PM = physiological maturity

to grain (Guindo, Wells, and Norman, 1994). Grain yield was about 6600 kg·ha⁻¹ or 49 percent of total dry matter production for this plant. Total dry matter production of upland rice grown on an Oxisol in Brazil increased nearly linearly as plants aged (Figure 3.4). Maximum vegetative dry matter was produced at about flowering and decreased by 21 percent due to assimilate translocation from leaves/stalks to grains. Grain yield was about 4900 kg·ha⁻¹ or 42 percent of total dry matter production for this plant. Protein metabolism dominates during vegetative growth phases, while carbohydrate metabolism dominates during reproductive growth phases (Murayama, 1995). Rates of protein, wall substances (cellulose and lignin), and carbohydrate accumulation in rice plants with growth stages are presented in Figure 3.5.

Maize vegetative dry matter consistently increased as plants aged (Figure 3.6). Dry matter accumulation for maize was different from that noted for lowland and upland rice (Figures 3.3 and 3.4), common bean (Figure 3.7), and soybean (Figure 3.8). Vegetative dry matter decreased after flowering for lowland and upland rice, common bean, and soybean, but total dry matter increased for maize. Both curves for dry matter of common bean and soybean were exponentially

quadratic, and dry matter production increased up to 80 days for common bean and up to 120 days for soybean. Thereafter, dry matter production declined in both of these crops. Decreases in dry matter yield were likely related to translocation of assimilates to grain as well as loss of older leaves senescencing. For both common bean and soybean, grain dry matter was not included. These results indicated that dry matter production differs among crop species as well as during crop growth stages. Data for vegetative dry matter production at harvest and grain yield concerned with Figures 3.3 to 3.8 are provided in Table 3.4. Among cereals, dry matter production was related to grain yield. For example, maximum dry matter was produced by maize, and this crop also produced higher grain yields than the other crops. Lowland rice was second in dry matter production as well as in grain yield. However, such trends were not observed among legumes. For example, soybean produced higher dry matter than common bean but produced less grain and had a lower harvest index than common bean.

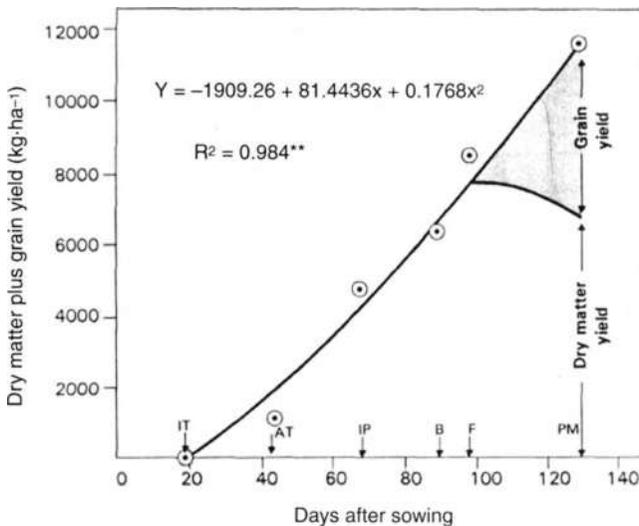


FIGURE 3.4. Dry matter accumulation and grain yield of upland rice grown in central Brazil on an Oxisols. Source: Reproduced from Fageria, 1998. Note: IT = initiation of tillering; AT = active tillering; IP = initiation of panicle; B = booting; F = flowering; and PM = physiological maturity

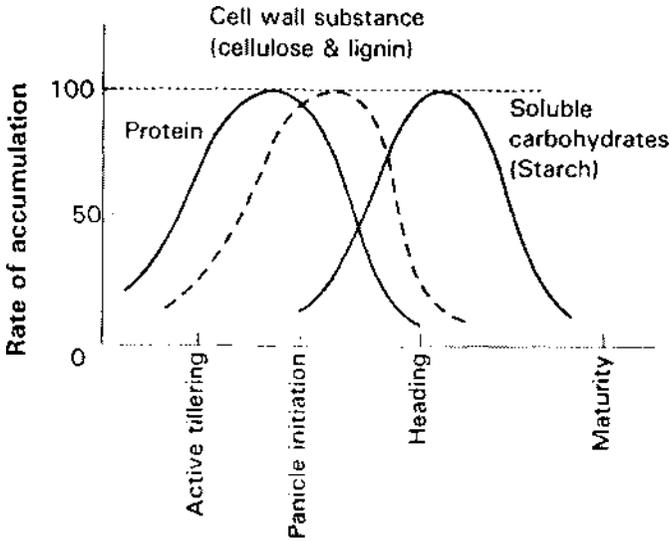


FIGURE 3.5. Accumulation rates of major organic substances in rice. *Source:* Reproduced from Murayama, 1995, with permission from Food and Agriculture Policy Research Center, Tokyo, Japan.

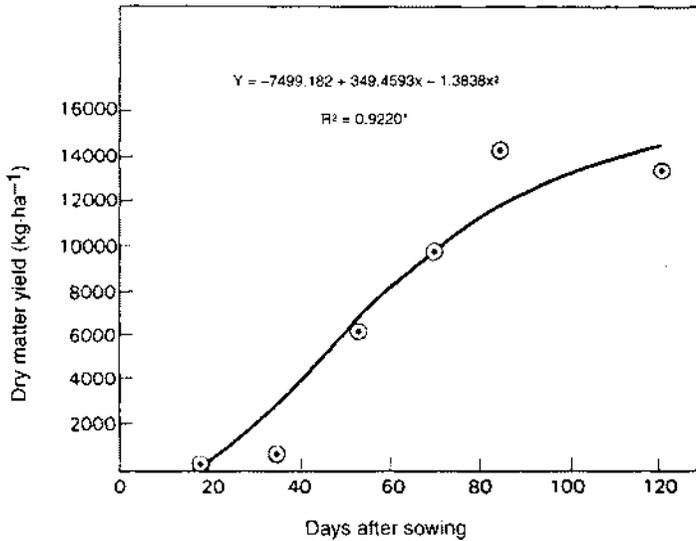


FIGURE 3.6. Dry matter production of maize grown in central Brazil on an Oxisol. *Source:* Reproduced from Fageria, 1998.

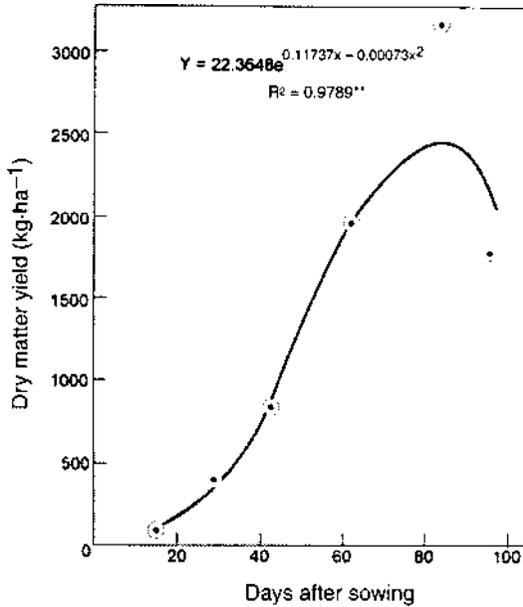


FIGURE 3.7. Dry matter production of common bean grown in central Brazil on an Oxisol. Source: Reproduced from Fageria, 1998.

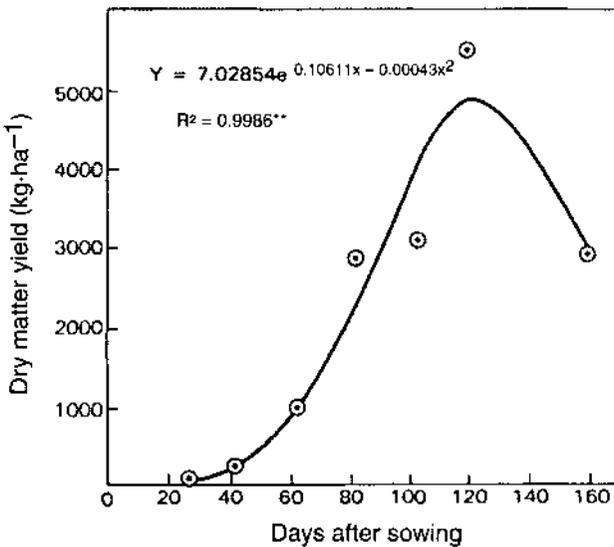


FIGURE 3.8. Dry matter production of soybean grown in central Brazil on an Oxisol. Source: Reproduced from Fageria, 1998.

TABLE 3.4. Shoot (straw) dry weight, grain yield, and harvest indexes of five annual crops grown on an Oxisol in central Brazil.

Crop species	Shoot dry weight (kg·ha ⁻¹)	Grain yield (kg·ha ⁻¹)	Harvest index
Upland rice	6642	4794	0.42
Lowland rice	9611	6862	0.42
Maize	13670	8148	0.37
Common bean	1773	1674	0.49
Soybean	2901	1323	0.31

Source: Fageria, 1998.

Unlike self-pollinated cereals in which improved partitioning of dry matter resulted in higher grain yields, similar improvements have not been obtained for grain legumes. Cereals are generally more responsive to increased soil inputs such as N fertilization, which accounts for improved cultivar performance through selection for responsive genotypes (Kelly, Kolkman, and Schneider, 1998). It has been widely reported that dry matter production of cereals such as rice, wheat, and maize is twice that for legumes such as soybean, common bean, and adzuki bean (Osaki, Shinano, and Tadano, 1992; Shinano, Osaki, and Tadano, 1994). It has been postulated that the low productivity of soybean was generally due to high contents of protein and lipids in seeds, because production of these compounds from photosynthates requires large amounts of energy (Yamaguchi, 1978). Based on studies of growth efficiency in harvesting organs and in whole plants during vegetative growth stages, low productivity of Leguminosae was mainly ascribed to high respiratory losses of carbohydrates from leaves and stems and not from harvested organs (Shinano et al., 1991; Shinano, Osaki, and Tadono, 1993), in contrast to findings reported by Yamaguchi (1978).

Tanaka and Osaki (1983) fed ¹⁴CO₂ to whole rice, wheat, maize, soybean, and common bean plants before analyzing for release of ¹⁴CO₂ from plants. They reported that larger amounts of ¹⁴CO₂ were released from soybean and common bean plants than from rice, wheat, and maize. Soybean also respired larger amounts of ¹⁴CO₂ from storage substances than did rice (Shinano et al., 1991). These results indicated that legumes consume larger amounts of current

photosynthates and/or temporary storage substances for respiration in leaves and stems than Graminaea plants. Further, dry matter production efficiency per unit N absorbed was reported to be lower in legumes than in cereals (Osaki, Shinano, and Tadano, 1992). This was ascribed to low growth efficiency of shoots but not to nodulation and low growth efficiency of grains (Osaki, Shinano, and Tadano, 1992; Shinano, Osaki, and Tadano, 1995). Shinano, Osaki, and Tadano (1994) suggested that when $^{14}\text{CO}_2$ was fed to leaves of rice and soybean, the amount of $^{14}\text{CO}_2$ released from soybean leaves was larger than that for rice under light conditions, because of higher photorespiration of soybean. In addition, photosynthesized C in leaves of soybean was more distributed into organic and amino acids than for rice (Shinano, Osaki, and Tadano, 1994). Accordingly, it has been hypothesized that photosynthesized C distribution mechanisms differ between cereal and legume crops (Nakamura et al., 1997). That is, photosynthesized C was actively distributed into tricarboxylic acid (TCA) and amino acid pools in legume crops grown under light, which resulted in higher respiratory rates compared to cereal crops. Higher proportions of photosynthesized C were distributed into carbohydrate pools, and photorespiratory activity was lower in cereals than in legumes.

Table 3.5 relates lowland rice dry matter production, grain yield, total biological yield, and harvest index to different levels of N when grown on an Inceptisol in central Brazil. Dry matter production, grain yield, and total biological yield increased as level of N increased. Harvest index also increased quadratically with increases of N, but responses were not significantly different. That is, grain yield was related to dry matter production and harvest index in a quadratic fashion, and application of adequate N is one management practice that is needed to improve dry matter and grain yields in annual crops.

DURATION OF REPRODUCTIVE GROWTH PERIOD

Duration of the reproductive growth period is very important because numbers of grains for plants are determined during this period. It has been reported that numbers of spikelets per ear in cereal crops can be increased by increasing length of the reproductive growth period (Yoshida, 1972). In grain crops (cereals), inflorescences and

TABLE 3.5. Shoot (straw) dry weight, grain yield, total biological yield, and harvest index of lowland rice grown on an Inceptisol in central Brazil.

N Rate (kg-ha ⁻¹)	Shoot dry weight (kg-ha ⁻¹)	Grain yield (kg-ha ⁻¹)	Total biological yield (kg-ha ⁻¹)	Harvest index
0	5278	3678	8956	0.41
30	6764	4281	11045	0.39
60	7294	5602	12896	0.43
90	7303	5647	12949	0.44
120	8215	6344	14559	0.44
150	8623	6362	14986	0.42
180	9060	6372	15433	0.41
210	9423	6389	15812	0.40
R ²	0.96 ^a	0.97 ^a	0.98 ^a	0.58 ^b

Source: Fageria, 1998.

^aSignificant at the 1 percent probability level

^bNonsignificant

leaves grow at the same time. Therefore, distribution of assimilates between inflorescences and leaves will also determine sizes of inflorescences. Most high-yielding rice cultivars are known to have small flag leaves. This is because flag leaves compete with developing inflorescences for assimilates.

Temperature and photoperiod are two major environmental variables that affect length of the preflowering period. In general, high temperature accelerates and low temperature delays flowering, but extremely high temperatures can also delay flowering (Yin, Kropff, and Goudriaan, 1997). Longer vegetative time periods (to heading) resulted in higher barley grain yield, but longer heading to maturity periods had no effect on grain yield (Dofing, 1997). Longer pre-heading time periods appear necessary to develop adequate numbers of kernels per spike and sufficient numbers of leaves to provide photo-assimilate during grain fill.

DURATION OF GRAIN-FILLING PERIOD

The grain-filling period is the duration from anthesis to physiological maturity and beyond. After physiological maturity, no significant increases in wheat grain dry matter occurred (Mou and Kronstad, 1994). However, harvest index generally increases over time after anthesis in soybean (Speath and Sinclair, 1985), cotton (Sadras, Bange, and Milroy, 1997), sorghum and maize (Muchow, 1990a,b), barley (Goynes et al., 1996), and sunflower (Bange, Hammer, and Rickert, 1998). Grain filling generally results from translocation of photosynthate from source to sink. For example, 80 to 90 percent of carbohydrate for grain growth of many plants is derived from photosynthetic activity after anthesis, and in the case of wheat, only 10 to 20 percent of carbohydrate comes from available reserves in vegetative plant parts (Spiertz and Vos, 1985). Kernel weight was also correlated with grain-filling rate in wheat (Bruckner and Froberg, 1987). Wheat cultivars differ in kernel weight and rate and duration of grain filling (Darroch and Baker, 1990). Grain-filling period is also influenced by temperature and light (Grabau, Van Sanford, and Meng, 1990).

Sayre et al. (1998) reported grain-filling rates for 15 wheat genotypes to average from $145 \text{ kg}\cdot\text{ha}^{-1}$ per day for plots treated by fungicide (rust disease control) to $115 \text{ kg}\cdot\text{ha}^{-1}$ per day for plots without fungicide treatment. Figure 3.9 shows relationships between average daily temperatures on grain-filling period, as well as kernel weight and grain yield, of oat. For each of these traits, values decreased linearly as average daily temperature increased, but decreases in grain-filling period were less than for the other traits. Fageria (1998) reported relationships between N application rate and grain-filling rate in lowland rice grown on an Inceptisol in central Brazil. Nitrogen application increased grain-filling rate from $129 \text{ kg}\cdot\text{ha}^{-1}$ per day with no added N to $231 \text{ kg}\cdot\text{ha}^{-1}$ per day with $180 \text{ kg N}\cdot\text{ha}^{-1}$.

Longer grain-filling periods commonly result in higher yields for many plant species grown under optimum environmental conditions. Because rice grain size is physically limited, yield capacity is largely determined by number of grains per unit land area. Therefore, increasing grain filling period would be meaningful if number of grains per unit area does not limit rice grain yield. Hartung, Poneleit, and Cornelius (1989) reported that grain-filling duration and dry matter

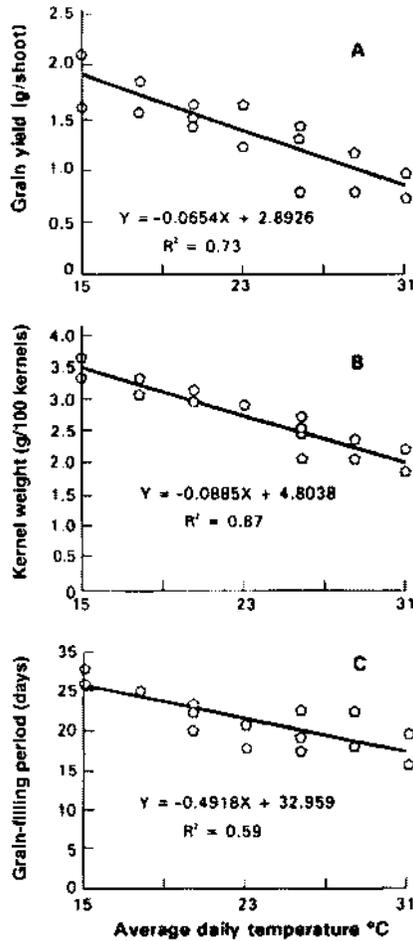


FIGURE 3.9. Linear regression of oat grain yield (A), kernel weight (B), and grain-filling period (C) as related to average daily temperature. *Source:* Reproduced from Hellewell et al., 1996, with permission from American Society of Crop Science, Madison, WI.

accumulation rates are associated with maize yield potential and might be used for indirect yield selection of this crop. Daynard, Tanner, and Duncan (1971) found that 70 to 80 percent of the yield differences among three maize hybrids were due to differences in the grain-filling period. A significant phenotypic correlation of 0.8 was

reported between grain yield and grain-filling period (Cross, 1975). Egli (1981) reported similar associations for seed growth characteristics of several plant species, particularly for those plants with seed sizes in excess of 250 mg per kernel. Yield improvements for maize achieved in long-term recurrent selection procedures have been associated with increased grain-filling period duration (Crosbie, 1982). Spiertz, Tem, and Kupers (1971) and Daynard and Kannenberg (1976) reported positive correlations between length of grain-filling period and grain yield in spring wheat and maize hybrids. However, Dofing (1997) reported that longer vegetative periods (time from sowing to heading) resulted in higher grain yields for barley, but longer heading to maturity periods had no effect on grain yields. In addition, faster grain-fill rates resulted in higher grain yields and shorter grain-filling periods (Dofing and Knight, 1994). Longer preheading periods appear necessary to develop adequate numbers of kernels per spikelet and sufficient numbers of leaves to provide photoassimilate during grain fill. Improved productivity of new oat cultivars has been due to short grain-fill periods and increased panicle filling rates (Peltonen-Sainio, 1991). Board, Wier, and Boethel (1994) reported that soybean grain yield reductions were caused by reduced seed size from shorter effective grain-filling periods and slower seed-filling rates. Effective seed-filling periods are that part of the seed-filling period whereby seed dry matter accumulates at linear rates to increase final seed sizes (Gbikpi and Crookston, 1981).

Seed-filling rate is the dry matter accumulation rate during the period of linear seed filling (Board, Wier, and Boethel, 1997). Further, C:N balances during grain filling or ripening periods are important in determining final yields of field crops. Generally, C accumulation in harvested organs occurs mainly during ripening, while N accumulation in harvested organs occurs largely from leaves that accumulate N before ripening. A small part of N in harvested organs also accumulates directly from N absorbed by roots during the ripening period (Osaki, Morikawa et al., 1993).

For cereals such as rice and wheat, grain N originates from both remobilization of vegetative tissue N and from active uptake and assimilation of N during grain fill. Remobilized N is usually the predominant N source for cereals grown under field conditions (Simmons, 1997). As N is remobilized from vegetative tissue, photosynthetic capacity of tissue decreases. The total loss of leaf areas and

termination of assimilate production should result in termination of grain fill (Frederick, 1997). Therefore, increasing plant N uptake during grain fill should theoretically delay leaf senescence and sustain leaf photosynthesis, resulting in longer grain-filling periods and heavier kernels.

Translocation of photosynthates from leaves to roots during grain filling decreases with plant age because sinks (organs to be harvested) require large amounts of photosynthates, and photosynthetic activity of lower leaves which commonly supplies photosynthates to roots decreases with mutual shading. As a result, root activity is assumed to limit N absorption during grain filling or maturation. In crops with high biological yields (e.g., maize, sugar beet, and sunflower), N absorption during maturation remains high (Osaki et al., 1995). This means that root ability to absorb N after flowering or grain filling is important for controlling productivity of some crops.

Gebeyehou, Knott, and Baker (1982) reported that the length of grain filling had significant positive correlations with kernels per spikelet ($r = 0.39^*$), kernel weight ($r = 0.56^{**}$), and grain yield ($r = 0.39^*$) for 16 durum wheat cultivars. Knott and Gebeyehou (1987) noted relationships between grain yield and length of grain filling in three durum wheat cultivars, and significant correlations occurred between grain yield and length of grain filling.

Grain sink capacity (potential of grains to achieve maximum mass) is genetically determined for plants grown under optimum growth conditions. However, actual grain capacity for plants grown under field conditions can be mediated by environmental perturbations such as water deficiency and heat stress. Delayed sowings in temperate climates caused slower rates of grain filling, shorter duration of grain filling, and decreased final weights of maize kernels (Cirilo and Andrade, 1996). Decreased irradiation and temperature 19 days after silking to physiological maturity reduced amounts of assimilates available for grain filling sufficient to decrease kernel weight (Cirilo and Andrade, 1996). Grain dry matter accumulation depends on rate and duration of crop growth, and availability of assimilate reserves from other plant parts. Potential sink strength for assimilates of grain is established during the lag phases of grain development when endosperm cell division is occurring (Reddy and Daynard, 1983). A shortage of assimilate supply or unfavorable environmental conditions during grain filling affects potential kernel size in maize (Jones et al.,

1996). Increased temperatures during grain filling also increase metabolic rates and sink strengths of maize kernels, and rates of grain filling (Jones, Ouattar, and Crookston, 1984). Moreover, several authors have suggested that reduction in assimilate supply to maize kernels induces early black layer formation to decrease grain filling duration and kernel size (Tollenaar and Daynard, 1978; Afuakwa, Crookston, and Jones, 1984; Cirilo and Andrade, 1996).

Temperature has large effects on grain filling and yield components. Hellewell et al. (1996) studied the effects of temperature treatments during grain filling on oat grain yield and yield components by growing three genotypes with varying maturity (early, mid, and late season) in controlled environmental chambers with varying planting dates to synchronize heading date among cultivars. At heading, each cultivar divided into nine treatments of day-night temperature combinations of 31, 23, and 15°C. Temperature treatments were imposed until plants were fully mature. Grain yield was 87 percent, kernel weight 51 percent, grain-fill period 27 percent, and grain-filling rate 45 percent greater for plants grown at 15°C day temperature than at 31°C day temperature with night temperature of 15°C. For night temperature, grain yield was 24 percent, kernel weight 12 percent, and grain-filling period 27 percent greater at 15°C night temperature than at 31°C night temperature with day temperature of 15°C. Figure 3.9 shows relationships between temperature and grain yield, kernel weight, and grain filling for oat.

MANAGEMENT STRATEGIES FOR IDEAL YIELD COMPONENTS

Environment, management, and genotypes interact to determine overall yields of crops. This means ideal yield components can be achieved through ideal combinations of favorable plant growth environments, adoption of adequate management practices, and use of appropriate genotypes. Among environmental factors, adequate moisture supply and optimum temperature and solar radiation are important in determining yield components and consequently yield. From the vast amounts of rainfall, temperature, and solar radiation data, it should be possible to adjust sowing dates and adopt appropriate plant species to determined environmental variables. The key aim to optimize crop productivity by matching ontogeny (sequence of

development stages) to weather resources of the environment (duration of favorable temperature, water supply, and solar radiation), and to minimize unfavorable extremes during vulnerable stages of growth (Summerfield et al., 1997). For annual crops, it is well understood that water deficiency and extreme temperatures during flowering reduces grain yield more than any other stage of growth. Hence, sowing date may be adjusted so that the most sensitive growth stage does not coincide with potential unfavorable weather conditions. Other options may be to use cultivars with different growth cycles, in which the most sensitive growth stage does not occur during anticipated stress periods. Planting drought-resistant and extreme-temperature-resistant plant species or cultivars is another strategy that can be used to reduce risk of crop yield losses due to prevailing stresses.

Early-flowering wheat cultivars are favored in regions that experience late-season heat stress. Such cultivars are better able to avoid reductions in kernel weight due to high temperature stresses during grain filling (Bruckner and Frohberg, 1987). Genotypic adaptation is especially important for short-season growth regions, in which sufficient heat units may not be available for crops to reach maturity. In such environments, inclement weather during harvest may result in complete losses of crops. However, early maturity in such environments is associated with reduced grain yield (Dofing, 1995). Therefore, reasonable breeding objectives would be to increase grain yield while keeping time to maturity constant.

Use of adequate levels of fertilizers, plant density, and plant spacing is important in producing ideal yield components. For example, N and P are important nutrients that determine numbers of panicles or grains produced per unit area. A typical example for increased numbers of panicles with applications of N of lowland rice grown on an Inceptisol in central Brazil is presented in Figure 3.10. Maximum numbers of panicles were obtained with applications of about 200 kg N/ha. Plants grown with low levels of N had higher spikelet sterility compared to higher levels of N (Figure 3.11). Spikelet sterility was about 35 percent for plants grown with zero added N, and was reduced to 28 percent with 210 kg N/ha. Small percentages (<15 percent) of floret sterility should be considered normal, as all florets in an ear do not set. This means that adequate N can improve rice grain yield by increasing numbers of panicles per unit area and reducing spikelet sterility. Nitrogen accumulation in dry matter and grain

PHYSIOLOGY OF CROP PRODUCTION

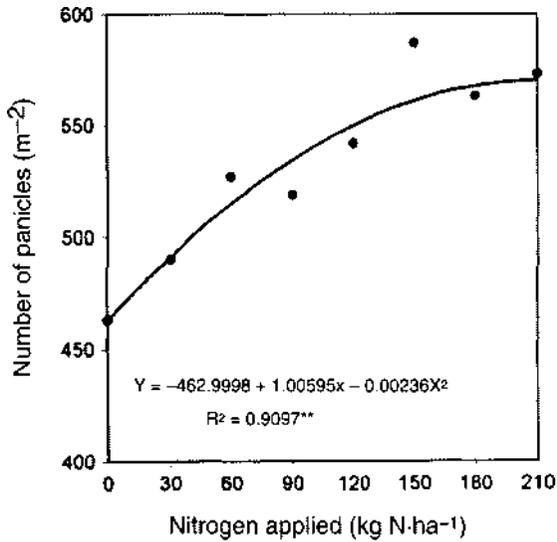


FIGURE 3.10. Relationship between N applied and number of panicles in lowland rice grown on an Inceptisols in central Brazil. *Source:* Reproduced from Fageria, 1998.

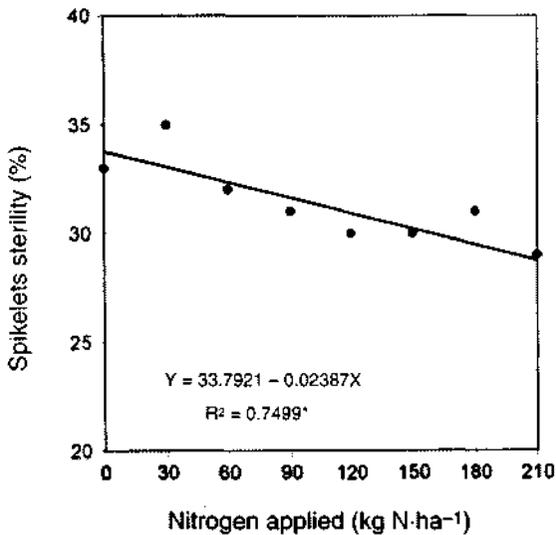


FIGURE 3.11. Relationship between N applied and spikelet sterility in lowland rice. *Source:* Reproduced from Fageria, 1998.

increased dry matter as well as grain yields of lowland rice grown on an Inceptisol in central Brazil (Figures 3.12 and 3.13). Among micro-nutrients, B is important in reproductive development of higher plants and reduces spikelet sterility. Subedi, Budhathoki, and Subedi (1997) reported strong wheat genotypic responses to B applications, and genotypic variations were evident. Boron at $1 \text{ kg}\cdot\text{ha}^{-1}$ reduced numbers of late ears, increased numbers of grains per ear, and increased grain yields in B-responsive wheat genotypes. However, added B did not influence B-tolerant genotypes. This means that addition of adequate amounts of B in B-deficient soils and use of B-tolerant genotypes are two attractive strategies for improving crop yields of annual crops.

The special distribution of plants in crop communities is an important determinant of yield, and many experiments have been conducted to determine spacing between rows and between plants within rows to maximize yield (Duncan, 1986; Egli, 1988). Two general concepts are frequently used to explain relationships between row spacing, plant density, and plant yield. First, maximum yield can be obtained only if plant communities produce sufficient leaf area to

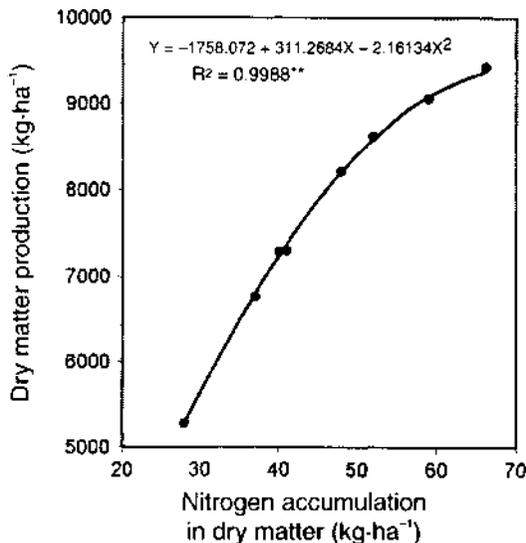


FIGURE 3.12. Nitrogen accumulation in dry matter and dry matter yield of lowland rice grown on an Inceptisol in central Brazil. *Source:* Reproduced from Fageria, 1998.

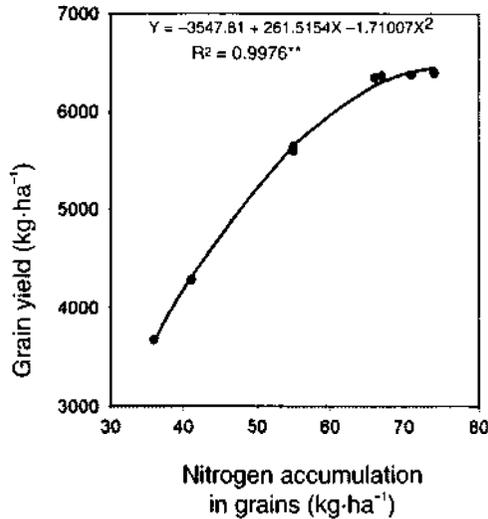


FIGURE 3.13. Nitrogen accumulation in grains and grain yield of lowland rice grown on an Inceptisol in central Brazil. *Source:* Reproduced from Fageria, 1998.

provide maximum light interception during reproductive growth (Johnson, Green, and Jordan, 1982). Second, equidistant spacing between plants will maximize yield because it minimizes interplant competition. Duncan (1986) defined three phases of soybean yield responses to increased plant density. Phase I covered ranges of plant densities where no competition among plants occurs, and yield is directly proportional to plant density (e.g., yield per plant is constant). Phase II begins at plant densities sufficiently large to intercept essentially all light at full canopy and is terminated at densities where further increases in density cause no increases in yield. Phase III includes all plant densities where increased competition among plants exists.

CONCLUSION

For maximum or highest potential yield of crop species or cultivars, it is important that crop species or cultivars sown have adaptability to growing environments for which the plants will be grown and biotic and abiotic stresses can be effectively controlled. Grain yield represents the summation of numerous physiological processes

and morphological developments, and these processes should be understood to measure or achieve highest yield potentials. Annual crop growth cycles are divided into three growth stages: vegetative, reproductive, and grain filling. In the vegetative growth stage, canopy architecture needs to be defined. This includes numbers of tillers and leaf area index. During vegetative growth, most photosynthetic capacities and yield capacities such as numbers of panicles or heads should be determined. Under optimum growth conditions, the contribution of preanthesis photosynthate reserves to final grain weight was 5 to 10 percent in wheat and 20 percent in barley (Evans and Wardlaw, 1976). Bingham (1969) noted that long vegetative growth periods often resulted in high grain yields of wheat. However, Sharma (1992) reported that combinations of short vegetative growth periods and long grain-filling periods might produce high grain yields for wheat. The vegetative phase duration has been positively correlated with leaf area and increased source size. Photosynthetic capacity as well as yield capacity is influenced by crop and environmental conditions. In the reproductive growth stage, numbers of grains need to be estimated (i.e., sink size) so that potential storage capacity for individual crops may be determined. Nearly all stem growth in cereal crops occurs during the reproductive growth stage, which becomes competitive with developing inflorescences (Evans and Wardlaw, 1976). Numbers of grains are very sensitive to N deficiency, drought, and extreme low and high temperatures. During the reproductive growth stage, division growth stage (about one week before flowering) is very sensitive to adverse environmental conditions, and numbers of grains are reduced. Longer vegetative growth periods or more rapid leaf area development during this phase increase source size, while longer grain-filling periods increase yield if sufficient sources of assimilate are present (Corke and Kannenberg, 1989). During grain filling, weights of grains are determined from up to one week to ten days after flowering. This is a very sensitive period of time for high potential yield. During this phase, potential grain storage capacity is determined by final yield. Any adverse environmental factors such as low radiation, N deficiency, low and high temperatures, and drought lower grain weights as well as increase grain sterility to reduce yield. This means management strategies such as using adequate levels of nutrients, especially N, adequate moisture, adjusting planting dates to avoid extreme low and high temperatures, and using

drought-resistant and nutrient-efficient cultivars can improve annual crop grain yields.

Economic yield of crops is determined by two parameters, namely, biological yield and harvest index. Biological yield is a function of growth duration and crop growth rate at successive growth stages. Harvest index is controlled by partitioning of photosynthates between harvested and nonharvested organs during plant growth cycles (Tanaka and Osaki, 1983). Significant changes in partitioning of photosynthate in crop plants (expressed as harvest index) have been important for changing grain yields. An important feature of changes in harvest index is the N budget for plants that must accompany changes in harvest index. N availability and the relative priority given to grain production help determine desired harvest indexes (Sinclair, 1998). Thus, economic yield is closely related to growth processes.

Breeding for physiological efficiency has been proposed as an approach to improve crop yield (Wallace et al., 1993). Days to maturity is the most important physiological trait affecting that outcome. All crop plants have specific growth rates. Through genetic manipulation, growth rates can be increased. However, increasing growth rates do not necessarily translate into higher seed yields unless greater amounts of photosynthate from vegetative biomass are partitioned to seeds. Indirect selection for the three major physiological traits affecting yield, namely, biomass, harvest index, and days to maturity, should result in improved yields (Wallace et al., 1993). Simultaneous selection of many traits is required because genetically established interrelationships occur among these physiological traits. Increases in maturity result in increased biomass, whereas increases in harvest index result in decreases in maturity and decreased biomass (Kelly, Kolkman, and Schneider, 1998; Kelly, Schneider, and Kolkman, 1999). Each of these physiological traits and their correlations among themselves can be quantified by yield system analyses of yield trial data (Wallace and Yan, 1998). Long-term direct selection for yield will gradually exploit the most useful genetic variability for harvest index and maturity.

Chapter 4

Photosynthesis and Crop Yield

INTRODUCTION

Photosynthesis is the basic process underlying plant growth and production of food, fuel, and fiber required to sustain life (Tolbert, 1997). An understanding of photosynthesis is therefore necessary to appreciate processes that determine yield in agriculture, forestry, ecology, and many other fields. This most important biochemical process in green plants, which literally means building by light, probably evolved 3500 million years ago (Shopf, 1993). In general, photosynthesis is the process by which plants synthesize organic compounds from inorganic substances using light. During photosynthesis, C from atmospheric carbon dioxide (CO_2) is fixed to become part of many organic molecules that constitute plant tissues. Because of this, total dry matter production of crop plants is correlated with photosynthetic rates integrated over plant growth cycles. Yield is related to total dry matter for many plants, especially associations with harvest index (see Chapter 3).

Light energy is converted into chemical potential energy when processes of photosynthesis occur. Chemical products of photosynthesis are translocated to sites of utilization and are incorporated into plant parts of economic interest such as grain in annual crops. Efficiency of light energy conversion to economic products depends on various factors such as CO_2 supply, light intensity, light interception, soil fertility level, water availability, temperature, and genetic factors related to the plant itself (Berry and Bjorkman, 1980; Eastin and Sullivan, 1984). Detailed discussion of these factors has been provided by Moss (1984). In photochemical reactions, carbohydrates are produced, and O_2 and water are released according to the following equation: