

## Chapter 1

# Plant Canopy Architecture

### *INTRODUCTION*

Canopy architecture can be viewed as a visible but momentary expression of plant form (Tomlinson, 1987). When used to describe plants, *architecture* refers to the spatial configuration of the above-ground plant organs and implies that this configuration has functional significance (Campbell and Norman, 1990; Lynch, 1995). The concept of plant canopy architecture is, in many ways, an abstraction that relates plant form to an orderly, genetically determined “growth plan.” The relationship between genetic encoded information and the resulting canopy architecture is analogous to that between a blueprint and the building it represents. Unlike buildings, plant canopies are dynamic and constantly changing with time and space in response to their environment.

A primary function of plant canopies is to intercept radiation to drive photosynthesis and other metabolic processes. This interception occurs with varying degrees of efficiency, which is determined chiefly by leaf area, configuration relative to the sun, and to a lesser extent the spatial arrangement of leaves (Duncan, 1975). Other important morphological canopy characteristics include plant height, tillering, branching patterns, and sizes and shapes of individual leaves. At least 90 percent of the biomass of higher plants is derived from CO<sub>2</sub> assimilated through photosynthesis (Zelitch, 1982). Because crop growth and yield are determined largely by photosynthesis, they are also highly dependent upon the amount of light intercepted by the canopy. Therefore, in environments in which light is the most limiting factor to crop growth and production, canopy properties that lead to greater interception of sunlight generally increase photosynthesis, and consequently grain or dry matter yield. Conversely, those that lead to poor light interception result in lower growth and yield.

When speaking of plant canopies or other plant features, it is often useful to have a mental picture of an ideal form. Early humans preferentially selected individuals with certain desirable attributes (Stoskopf, 1981), which was the earliest form of plant domestication. This process continues today with modern plant breeders, who often have a mental concept of an ideal plant, or *ideotype*, that guides their breeding programs. The goal of “ideotype breeding” is to define theoretically the most efficient plant type for a particular crop and environment, and then to breed toward this goal. Donald (1968) defined ideotype as a biological model that is expected to perform or behave in a predictable manner within a defined environment. More specifically, a “crop ideotype” is a plant model that is expected to yield a greater quantity and/or quality of grain, oil, or other useful product in a particular environment when developed as a cultivar. *Environment* from a plant breeding point of view can be defined as the integrated influence of all nongenetic variables affecting phenotypic expression of crop species or genotypes (Saeed and Francis, 1984).

It should be apparent that what is ideal for one environment would not be ideal for another. For example, a plant for hot and dry environments may not be ideal for cold and wet environments. Therefore, development of a crop ideotype has to take into account what is termed “genotype by environment interaction,” or G×E interaction (Kang, 1998; Rao et al., 2002). The term G×E interaction stems largely from elementary statistical analysis of variance for yield among different crop genotypes for a particular species grown under a variety of environments. These environments often range from low stress to high stress. An elementary statistical yield model that can be used to describe yield response to genotype and environment is

$$Y = \mu + G + E + G \times E + \varepsilon \quad (1.1)$$

where  $Y$  equals yield for a particular treatment combination (yield of a particular genotype in a particular environment);  $\mu$  equals overall mean yield;  $G$  equals the genotypic effect upon yield;  $E$  equals the environmental effect upon yield; and  $\varepsilon$  equals random error. Depending upon the crop, physiological trait, and range of environments, G×E can be very large or practically nonexistent. An understanding of the importance of G×E therefore necessitates physiological studies on the response of different plant processes to different environmental

factors. Only then can an ideotype, or model, be developed. Several workers considered  $G \times E$  interaction as linear functions of environment and proposed regression of yield of a genotype on the mean yield of all genotypes in each environment to evaluate genotype performance stability (Eberhart and Russell, 1966; Finlay and Wilkinson, 1963; Perkins and Jinks, 1968).

On the basis of several physiological studies, Donald (1968) described a wheat ideotype for a favorable environment that had a short stem, relatively few, small, erect leaves, a large ear with many florets per unit of dry matter of the crop, an erect ear, awns, and a single culm. Asana (1968) also described a wheat ideotype suitable for dryland conditions.

One of the major benefits of ideotype breeding is that breeders are forced to define their goals and strategies in advance (Ortiz and Langie, 1997). For example, based upon the morphological design postulated by Donald (1968), it was concluded that a successful crop plant needed high competitive ability relative to its mass and high efficiency relative to its use of environmental resources. It has been shown that high-yielding cultivars of barley and rice are suppressed or eliminated in mixtures (Sinha and Swaminathan, 1984). Therefore, a breeder would have to envisage different ideotypes when breeding crops for monoculture as opposed to mixed cropping systems, since the two systems represent two different kinds of competition. Using the ideotype approach, breeders select for and not against specific phenotypes.

Many examples exist for achieving yield increases through the use of ideotype breeding for improved canopy architecture. In 1989, the International Rice Research Institute (IRRI), located in the Philippines, conceptualized and developed new plant ideotypes for annual upland, rainfed lowland, and direct-seeded irrigated rice (Table 1.1). Figure 1.1 shows the architecture of IRRI's ideotype for irrigated rice, which was designed to produce fewer tillers than the improved cultivars commonly grown today, but almost every tiller will bear panicles. The new rice ideotype, which has a vigorous root system to draw nutrients from the soil, will be appropriate for both direct seeding and transplanting.

Ideotypes have also been suggested for the development of higher-yielding dry or common bean cultivars. Denis and Adams (1978) suggested an ideotype that consists of a relatively large plant with

TABLE 1.1. Characteristics of ideotypic rice plants.

<b>Upland rice</b>	<b>Rainfed lowland rice</b>	<b>Direct-seeded irrigated rice</b>
130 cm tall	130 cm tall	90 cm tall
Very sturdy stems	Very sturdy stems	Very sturdy stems
5-8 panicles per plant	6-10 panicles per plant	3-4 panicles per plant
150-200 grains per panicle	150-200 grains per panicle	200-250 grains per panicle
Erect upper leaves, droopy lower leaves	Dark green, erect or moderately droopy leaves	Dark green, erect, thick leaves
Deep, thick roots	Extensive root system	Vigorous root system
100 days growth cycle	120-150 days growth cycle	100-130 days growth cycle
Multiple disease and insect resistance	Multiple disease and insect resistance	Multiple disease and insect resistance
3-4 t·ha <sup>-1</sup> yield potential	5-7 t·ha <sup>-1</sup> yield potential	13-15 t·ha <sup>-1</sup> yield potential
	Strong submergence tolerance	0.6 harvest index
	Strong grain dormancy	

*Source:* Adapted from IRRI, 1989.

numerous nodes, leaves, and reproductive structures. They also suggested ideotypes with more open canopy architecture to facilitate more uniform light interception throughout the canopy.

For maize, Mock and Pearce (1975) defined an ideotype with a leaf area index (LAI, the ratio of leaf surface to ground surface) > 4, with stiff, vertically oriented leaves located above the ear, and horizontally oriented leaves below the ear, in order to maximize light interception by the entire canopy. Ideotypes have also been described for several other crops such as barley (Rasmusson, 1987).

An analysis of canopy architecture of a crop or variety helps to explain how plants utilize their aerial environments. The interaction of the aboveground vegetation of a crop with the environment is largely controlled by canopy architecture (Welles and Norman, 1991) in terms of the distribution, area, and shape of leaves, stems, and inflorescences. This information can be useful to crop scientists interested

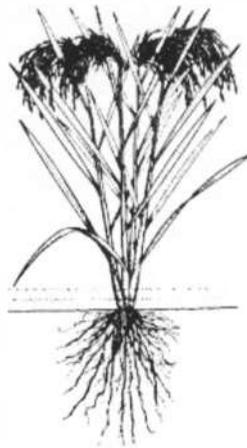


FIGURE 1.1. Schematic ideotype of direct-seeded irrigated rice plant. *Source:* Reproduced by permission of International Rice Research Institute, Los Baños, Philippines, 1989.

in improving morphological traits of annual crop cultivars for higher productivity. The objective of this chapter is to characterize ideal plant architecture, in terms of height, tillering, and leaf characteristics. We also discuss management strategies for ideal plant architecture and relate these to yield enhancement.

### ***PLANT HEIGHT***

Plant height is the distance from ground level to the tip of the tallest leaf for seedlings or juvenile plants. For mature plants, it is the distance from ground level to the tip of the tallest panicle, ear, or head in cereals and branch legumes. Short and sturdy culms, more than any other character, favor lodging resistance. Lodging is the permanent displacement of the stems from their upright position. There are three types of lodging: breaking of the stem, bending of the stem, and rolling, in which the whole plant is uprooted from the ground and falls over. A tall crop variety has greater bending momentum than a short one because of culm height. Early lodging of long, thin culms disturbs leaf arrangement, increases mutual shading, interrupts transport

of nutrients and photosynthates, causes grains sterility, and reduces yield (Jennings, Coffman, and Kauffman, 1979). Further, strong winds and rains during reproductive and grain filling stages of growth can cause lodging in annual crops. Lodging during the grain filling growth stage can reduce grain quality.

A short and sturdy culm also promotes favorable grain-to-straw ratios, adequate N responses, and high yield capacities. Increased N application is essential for higher yields but causes elongation of the lower internodes, making the crop more susceptible to lodging. In addition, planting date, row spacing, and seeding rate affect lodging in soybean (Willmot, Pepper, and Nafziger, 1989), as well as plant height, branch production, and basal pod height.

A standard evaluation system has been designed by IRRI for plant height, culm resistance, and lodging incidence of rice (Table 1.2). Similarly, Willmot, Pepper, and Nafziger (1989) devised a rating system for lodging for soybean and other legumes to evaluate lodging resistance (Table 1.3). The importance of lodging resistance to high yield capacity has long been recognized, but only in recent years has

TABLE 1.2. Standard evaluation system for rice for plant height, culm strength, and lodging incidence.

Scale rating	Plant height	Culm strength: Plants lodged	Lodging incidence: Area affected
0	Semi-dwarf	Strong	No lodging
1	Semi-dwarf: Lowland <110 cm and upland <90 cm	Strong: No bending	Less than 20 percent
3		Moderately strong: Most plants bending	20-40 percent
5	Intermediate: Lowland 110-130 cm and upland 90-125 cm	Intermediate: Most plants moderately bending	41-60 percent
7		Weak: Most plants nearly flat	61-80 percent
9	Tall: Lowland >130 cm and upland >125 cm	Very weak: All plants flat	More than 80 percent

Source: Adapted from IRRI, 1988.

TABLE 1.3. Rating scale for main stem and branch lodging in soybean.

Lodging score	Visual criteria
1	Almost all plants erect
2	Broken branches on 10 to 30 percent of plants
3	Plants leaning 30° plus 30 to 60 percent with broken branches
4	Plants leaning 45° plus 60 to 90 percent with broken branches
5	All plants leaning 60° plus 100 percent with broken branches

Source: Willmot, Pepper, and Nafziger, 1989. Reproduced by permission from American Society of Agronomy, Madison, WI.

this trait been effectively introduced in rice, wheat, barley, and sorghum. Lodging resistance is principally related to short stature, but it also depends on other characters such as culm diameter, culm wall thickness, and the degree to which leaf sheaths wrap internodes.

The creation of semi-dwarf cultivars spectacularly increased the yielding ability of many crops, such as rice and wheat. For example, Table 1.4 compares yields of older and taller traditional cultivars of upland rice to modern, semi-dwarf cultivars of Brazil. Yields of the modern cultivars are higher, in part, because they are less susceptible to lodging than the old ones. Similarly, lowland rice cultivars used in the Philippines have, over the past 70 years, become shorter, in addition to having smaller, more upright leaves and reduced sensitivity to photoperiod. Panicle weights initially became heavier, but later were made lighter with greatly increased panicle numbers.

A marked increase in harvest index and in grain production per day has been associated with reduced plant height and earlier maturity (Evans, Visperas, and Vergara, 1984). The heritability of dwarfism in cereals is high and is easy to identify, select for, and recombine with other traits. Although yield gains due to the introduction of dwarfing genes into cereals have been remarkable, little evidence exists for concomitant improvements in photosynthetic rate, crop growth rate, or kernel weight.

The introduction of semi-dwarf genes has been advantageous for yield, but extremely short plant stature is not at all advantageous, because leaves are very closely spaced on short culms, which causes high

TABLE 1.4. Plant height, grain yield, and lodging rating of traditional and modern upland rice cultivars under Brazilian conditions.

Cultivar	Plant height (cm)	Grain yield (kg-ha <sup>-1</sup> )	Lodging rating <sup>a</sup>
Traditional			
Rio Paranaíba	108	2780	3
Caiapó	105	2590	2
Guarani	98	2640	4
CNA 8054	108	2470	3
Average	105	2620	3
Modern			
Progresso	86	2620	1
CNA 8172	86	2860	1
CNA 8305	91	2990	1
Canastra	88	2870	1
Average	88	2840	1

Source: Morais, 1998.

<sup>a</sup>Higher values mean relatively more susceptibility to lodging and lower values mean more resistant to lodging.

shading within the plant canopy. Therefore, an optimum plant height is important, which may vary with plant species and environment.

### TILLERING

Tillers are the branches that develop from the leaf axils at each unelongated node of the main shoot or from other tillers during vegetative growth. The development of tiller buds after differentiation is greatly affected by environmental conditions, as well as by genotypic characteristics. The environment must be favorable for tiller development. It is essential that sufficient supplies of water, photosynthate, nutrients, and plant hormones are present, and that stress is minimal. The addition of plant nutrients is particularly important when soils have low fertility. Figure 1.2 shows the increase in tiller number with increasing levels of N in lowland rice grown on an Inceptisol of

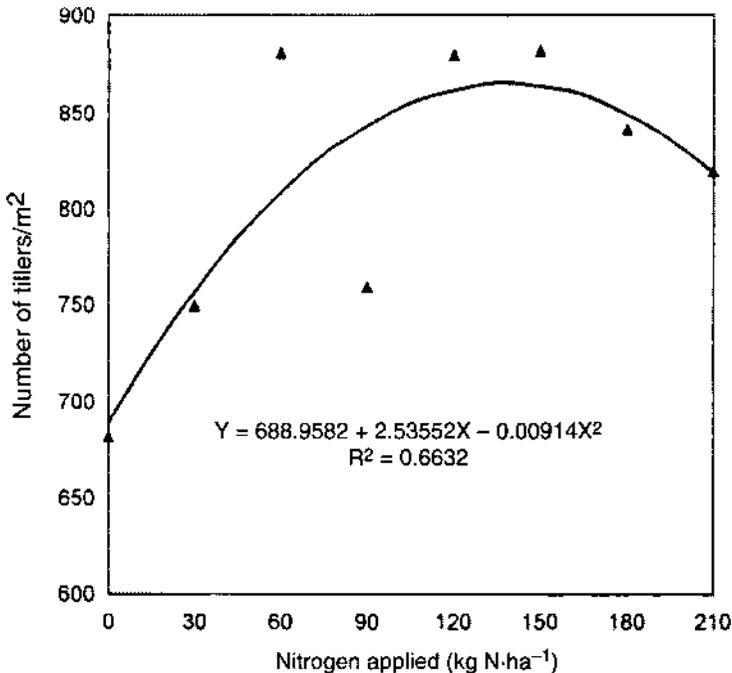


FIGURE 1.2. Relationship between nitrogen application and number of tillers in flooded rice grown on an Inceptisol of central Brazil. *Source:* Reproduced from Fageria, 1998.

central Brazil. Similarly, tiller number of upland rice increased with the application of P at  $75 \text{ mg}\cdot\text{kg}^{-1}$  of soil for an Oxisol of central Brazil (Table 1.5). Nutrients required for the growth of tiller buds of rice must come from the main stem, since tiller buds have neither roots to absorb inorganic nutrients nor leaves to carry out photosynthesis. Once tillers have emerged from the subtending leaf sheaths, they can perform photosynthesis and produce carbohydrates. Tillers can also absorb soil nutrients through their own roots after the third leaf has completely emerged, since roots appear at the prophyll nodes of tillers at this stage of growth (Handa, 1995).

Tiller number is quantitatively inherited. Heritability for tiller number has been low to intermediate, depending on the cultural practices and the uniformity of soil. Although often associated with early vigor in short-stature plants, tiller number is inherited independently

TABLE 1.5. Tiller number per pot under two levels of phosphorus in upland rice genotypes grown on an Oxisol of central Brazil.

Genotypes	0 mg P·kg <sup>-1</sup>	75 mg P·kg <sup>-1</sup>
CNA 6187	5	15
CNA 7645	5	16
CNA 7127	5	17
CNA7680	5	14
CNA 7864	5	18
Rio Paranaíba	5	17
Average	5	16

Source: Adapted from Fageria and Baligar, 1997.

from other major crop traits. In many crosses, tiller erectness or compactness is recessive to spreading culm arrangement (Jennings, Coffman, and Kauffman, 1979).

Whether tillering is governed through genetic, hormonal, or other mechanisms, the full expression of tillering or branching is determined predominantly by the supply of minerals and photoassimilates to the plants. Tiller survival and the production of an inflorescence are paramount to yield. The degree of interplant competition for minerals, photoassimilates, and water will determine how many tillers will reach maturity (Stoskopf, 1981). The proportion of tillers that survive to produce grain depends on the genotype, N fertility, water status, plant density, changes in light quality during crop growth duration, and plant spatial arrangement (Simmons, Rasmusson, and Wiersma, 1982; Simmons and Lauer, 1986; Lauer and Simmons, 1989). In cereals such as rice and wheat, tillering increases as plants develop until a maximum value is reached, after which it decreases. Figure 1.3 illustrates this relationship between plant age and tillering for lowland rice grown on an Inceptisol in central Brazil. Tillering started 18 days after sowing and followed a quadratic relation with crop growth duration. Maximum tillering, based on the quadratic function, was attained at 75 days after sowing, and decreased thereafter.

Decrease in tiller number after reaching a maximum has been attributed to the death of later tillers because of the inability to compete for light and nutrients (Fageria, Santos, and Baligar, 1997). In

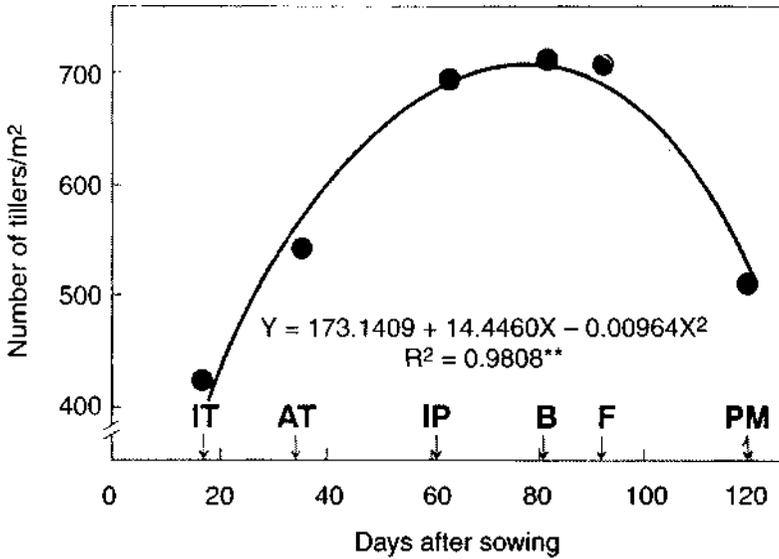


FIGURE 1.3. Relationship between plant age and tiller number in lowland rice. Source: Fageria, Santos, and Baligar, 1997. Reproduced by permission of American Society of Agronomy, Madison, WI.

addition, competition for photoassimilates begins between panicles and tillers after panicle development. As growth of many young tillers is suppressed, they may eventually senesce without producing seed (Dofing and Karlsson, 1993). Both shading of tillers and shifts in shoot photoassimilate partitioning patterns have been proposed as factors causing tiller death in grasses (Lauer and Simmons, 1985, 1989). Spiertz and Ellen (1972) reported that light enrichment reduced tiller mortality in perennial ryegrass.

Plant density is another important factor affecting tillering (Counce, Wells, and Gravois, 1992; Wu, Wilson, and McClung, 1998), because it affects competition for light and other resources (Liang, Muo, and Ran, 1986). As plant density and resource competition increase, the proportion of secondary and tertiary tillers in rice decreases (Hoshikawa, 1989). For many plant species, tillering is a mechanism for assuring that the amount of biomass produced is in balance with the amount of plant resources available. For example, Miller, Hill, and Roberts (1991) noted that tiller density in rice increased significantly as plant density increased from 122 to 458 plants/m<sup>2</sup>, while total

aboveground mass was not significantly different among the plant populations.

### LEAF CHARACTERISTICS

Leaf characters such as erectness, length, width, thickness, toughness, color, and senescence are often associated with yielding ability of plant species or cultivars. Among these characters, erect orientation of leaves is associated with high yielding capacity. Erect leaves permit greater penetration and more even distribution of light into the crop, and thus higher photosynthetic activity. Plants with upright leaves may require less physical space than plants with horizontal leaves and may be adapted to narrow row widths. Leaf angle has been closely correlated with N response in rice, barley, and wheat (Yoshida, 1972). Erect leaves seem to be the result of a pleiotrophic effect of the dwarf gene. Therefore, this trait follows simple recessive modes of inheritance. The erect leaf trait is highly heritable, easily observed at early flowering, and easy to visually rate in pedigree rows of fixed lines (Jennings, Coffman, and Kauffman, 1979).

Leaf thickness is also a desirable leaf trait. Thicker leaves usually have higher densities of chlorophyll per unit leaf area, and hence have greater photosynthetic capacities than thinner leaves (Craufurd et al., 1999). Vigorous leaf growth in crop plants has generally been associated with long-term gains in photosynthetic potential (Blum, Sullivan, and Nguyen, 1997). Plant size may provide substantial yield benefits. For example, rice leaf growth rate is lower compared with maize and barley. A better knowledge of underlying physiological mechanisms involved in limiting leaf growth in rice could facilitate progress in this direction. Lu and Neumann (1999) concluded that the lower growth rate of rice leaves was not associated with comparatively lower rates of epidermal cell production, but instead was associated with the production of smaller mature cells. In addition, this smaller size of rice leaf cells was not associated with less negative osmotic potentials in the cell expansion zone. However, comparative extensibilities of growing leaf tissues and cell walls decreased in the order of barley > maize > rice, and gave good linear correlations with leaf relative growth rates ( $r = 0.87^{**}$  and  $0.97^{**}$ , respectively). The data indicated that low cell wall extensibility limits maximum leaf growth rate in rice. Future introduction of increased wall extensibility

in rice might lead to increases in leaf growth potential, and conceivably to improved yields.

Leaf size is directly associated with leaf angle, with short leaves tending to be more erect than longer ones. Further, short leaves are usually more evenly distributed throughout the canopy, which permits less mutual shading of leaves and more efficient use of light for photosynthesis. As leaves become longer, they become more difficult for the midrib to support, and therefore tend to droop. Usually, dwarf cereal cultivars have short leaves and tall cultivars have long leaves, although some may have short leaves. These strong associations indicate that leaf length in both dwarf and tall cultivars is a pleiotrophic effect of genes for plant height (Jennings, Coffman, and Kauffman, 1979).

Many examples of higher yield being associated with smaller leaf size and more erect leaf angle distribution are available. Yield of perennial ryegrass was positively correlated with leaf length and LAI, and cultivars with erect foliage were more productive than those with planophile canopies (Rhodes, 1975). Similarly, maize yield has been greater for cultivars with erect canopies than for cultivars with more horizontal orientation (Pendleton et al., 1968). Light entering a canopy of erect leaves was spread over larger photosynthetic areas than in prostrate cultivars, resulting in greater photosynthetic efficiency (Redfearn et al., 1997).

Leaf width is less variable than length. Narrow leaves are more desirable than the wider ones due to more even distribution in the plant canopy. Similarly, thick leaves are associated with high yielding capacities of crop cultivars. However, this character is difficult to measure visually under field conditions and is generally not evaluated in breeding programs. Leaf thickness can be measured microscopically, but it is conveniently expressed as specific leaf area (area per mass) or specific leaf weight (mass per area).

Other leaf characters that have been associated with yield include leaf toughness, color, and senescence. Leaf toughness, which is important in preventing breaking during heavy wind and rain, is related to thickness and lignification of leaf tissues.

Senescence refers to degenerative changes normally associated with the declining phase of leaf, whole plant physiological activities, or both (Wolfe et al., 1988b). Senescence is of economic interest because it affects crop productivity by reducing the active photosynthetic area.



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where GLA = green leaf area per plant,  $t_1$  = initial time, and  $t_2$  = final time, and GDD = [(maximum temperature + minimum temperature)/2 - 10]. Growing degree-days is generally used in defining plant growth stage because it represents a better indication of plant development stage than calendar days (Neild and Seeley, 1977).

### **BREEDING AND MANAGEMENT STRATEGIES FOR IDEAL PLANT ARCHITECTURE**

Ideal plant architecture for higher yield can be achieved through plant breeding and the adoption of adequate cultural practices. It has been recognized that the spectacular yield increase of crops during the second part of the twentieth century have been attributed in almost equal measure to breeding and to the use of inputs.

#### ***Breeding***

The most important morphological characters that have been bred into high-yielding cereal cultivars, such as rice and wheat, are short, stiff culms for lodging resistance, and erect leaves for increased interception of solar radiation. Several examples of crop improvement through breeding for ideal plant architecture are provided.

#### ***Rice***

A typical example of breeding semi-dwarf high-yielding cultivars comes from IRRI. The tall tropical cultivar Peta from Indonesia and the subtropical semi-dwarf cultivar De-geo-woo-gen from Taiwan were crossed to produce the semi-dwarf 'IR 8', which produced a record yield of 11 t·ha<sup>-1</sup> and responded well to N rates up to 150 kg·ha<sup>-1</sup> at several locations in tropical Asia (Chang, 1976). Dissemination of this improved plant type throughout Latin America was initiated in 1968 by the Colombian-based program of the International Center of Tropical Agriculture together with National Research Institutes in the region (Cuevas-Perez et al., 1995). Scientists at IRRI and several national breeding programs combined most of the desired features in the improved plant type, including reduced height (about 100 cm), leaf erectness, short, dark green leaves, stiff culms, early maturity,

photoperiod insensitivity, N responsiveness, and high harvest index (Yoshida, 1981). The wide adoption of 'IR 8' and other high-yielding cultivars, such as 'IR 20' and 'IR 22', made it possible for the semi-dwarf cultivars to become important cultivars in Brazil, Colombia, Peru, Ecuador, Cuba, Mexico, Indonesia, Malaysia, Philippines, India, Pakistan, Bangladesh, and South Vietnam. By 1972-1973, semi-dwarf cultivars occupied a large part of the area planted to high yielding rice cultivars, including about 10 percent of the world total area and 15 percent of the area in tropical Asia (Chang, 1976). Today, high-yielding semi-dwarf cultivars predominate in most lowland rice-producing areas.

Work is in progress at IRRI and many other international and national research centers to further improve plant type, grain quality, and pest resistance (Khush, 1995). Figure 1.4 shows the development of modern high-yielding rice cultivars from formerly prevalent traditional cultivars, and ideotype rice plants of the future. As shown in Figure 1.4, the new plant type for irrigated rice was designed to attain yields of 12 to 13 t·ha<sup>-1</sup>. Yield improvement beyond 12 t·ha<sup>-1</sup> will require new plant architectures because of two major problems: The leaves responsible for grain filling will be shaded beneath a dense

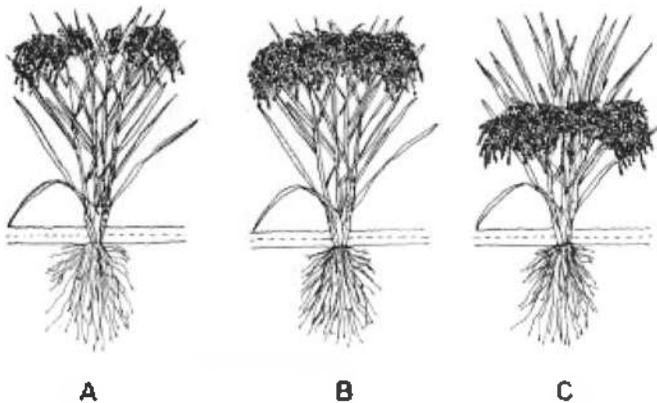


FIGURE 1.4. New plant types for irrigated rice. A: current generation of new plant types aimed at yields of 12 to 13 t·ha<sup>-1</sup>; B: same plant type but aimed at yields over 15 t·ha<sup>-1</sup>; and C: new generation plant type aimed at yields over 15 t·ha<sup>-1</sup>, but with greater light interception by leaves and resistance to lodging. Source: Reproduced by permission of International Rice Research Institute, Los Baños, Philippines, 1993.

cover of panicles, and the immense weight of panicles will result in serious lodging (Figure 1.4). A solution to both problems is to lower the panicle height in the canopy (Figure 1.4). Such adaptations may be relevant to other rice ecosystems as well as to other cereals (IRRI, 1993).

### *Wheat*

Modification of wheat plant architecture through breeding is another example of ideal plant type for improving yield of an important cereal (Byerlee and Curtis, 1988). Wheat yields increased significantly during the twentieth century, with an average global increase of 250 percent during the past 50 years (from 1 to 2.5 t-ha<sup>-1</sup>). This is remarkable when one considers that wheat yields remained practically unchanged during the first half of the twentieth century (Slafer, Satorre, and Andrade, 1994; Slafer, Calderini, and Miralles, 1996). Better plant architecture through plant breeding and better management practices are responsible for this accomplishment (Calderini and Slafer, 1998).

Detailed analysis of the decade from the mid-1980s to the mid-1990s (Slafer, Satorre, and Andrade, 1994) indicated that worldwide wheat yields might be approaching a ceiling, since average yields did not increase from 1990 to 1995. However, yield potential data of CIMMYT (Centro Internacional de Mejoramiento de Maize y Trigo, Mexico) cultivars developed since the 1960s (Figure 1.5) do not indicate a plateau. Indeed, the average increase per year was 0.9 percent (Braun, Rajaram, and Ginkel, 1997). This genetic progress for increasing yield potential was closely associated with increases in photosynthetic activity through the ideal plant canopy (Rees et al., 1993). Both photosynthetic activity and yield potential increased over the 30-year period by 25 percent.

Similarly, an estimated 50 percent of the increase in U.S. wheat yields from 1954 to 1979 can be credited to genetic improvement (Schmidt, 1984). Introduction of semi-dwarf cultivars of wheat had a large impact on productivity of wheat in the Corn Belt and the Great Plains of the United States, and is probably the major source of genetic gain in both regions (Feyerherm, Kemp, and Paulsen, 1988). Semi-dwarf cultivars were planted on more than 90 percent of the

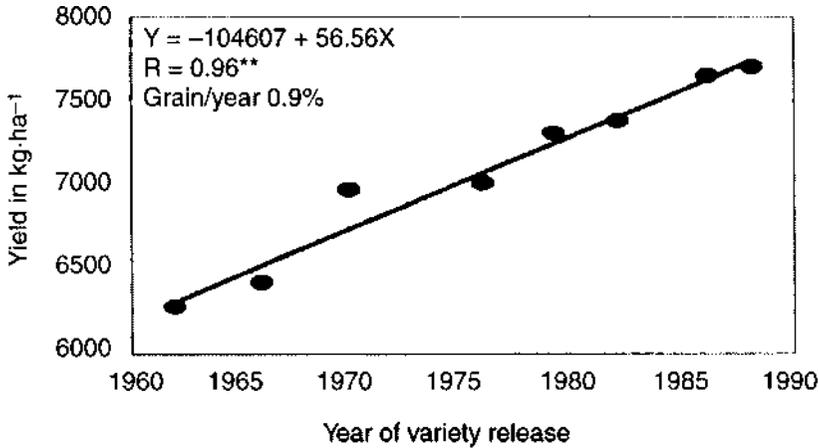


FIGURE 1.5. Mean grain yields for the historical series of bread wheat varieties for the years 1960 to 1990 at Cd. Obregon, Mexico. *Source:* Adapted from Rees et al., 1993.

area planted to wheat in the Corn Belt by 1979, when the genetic gain in productivity was as high as 74 percent (Siegenthaler, Stepanich, and Briggie, 1986). In the Great Plains states (Kansas, Nebraska, and Oklahoma), semi-dwarf cultivars occupied only 9, 1, and 38 percent, respectively, of the area planted to wheat, and genetic improvement for yield was only 45 percent. However, the area planted to semi-dwarf cultivars by 1984 increased to 70, 38, and 76 percent, respectively, in the three states, and genetic improvement increased to 61 percent (Feyerherm, Kemp, and Paulsen, 1988).

Since the beginning of the 1960s, grain yield of winter wheat has increased by about 120 kg·ha<sup>-1</sup> per year in France. This increase was mainly related to genetic improvement of cultivars and use of adequate levels of N (Gouis and Pluchard, 1997).

### *Maize*

Genetic improvement in grain yield of maize hybrids in North America and Europe during the last three to five decades of the twentieth century has been extensively documented (Tollenaar and Aguilera, 1992). Grain yield improvement of maize hybrids appeared to be the result of increased dry matter accumulation. Increased dry

matter may be attributable to either increased absorption of incident photosynthetically active radiation (PAR) and/or improved efficiency of converting absorbed PAR into dry matter. Some evidence indicates that modern hybrids absorb more of the seasonal incidence PAR than the older hybrids. Maximum LAI for modern hybrids was larger than for older ones, and leaves of modern hybrids stay green longer during the final phase of the life growth cycle (Tollenaar and Aguilera, 1992). Full season maize landraces adapted to the lowland tropics are typically tall, leafy, and prone to lodging, and have low harvest indexes (Goldsworthy, Palmer, and Sperling, 1974). During initial stages of maize improvement at CIMMYT, reduction in plant height was a priority (Fischer and Palmer, 1984), and reduced plant height has continued only as a secondary trait in breeding activity. Johnson et al. (1986) reported that 15 cycles of recurrent selection for reduced height in the lowland tropical maize population reduced plant stature by 37 percent and crop duration by 7 percent, and increased the proportional allocation of total biomass to husks, ears, and silks at the 50 percent silking stage. At the same time, researchers observed that grain yield, harvest index, and optimum plant density for grain yield each increased by 50 to 70 percent. Lodging was also substantially reduced. Similarly, Edmeades and Lafitte (1993) reported that lodging in maize declined from 39 to 10 percent with 18 cycles of recurrent selection.

### *Other Crops*

Bridge, Meredith, and Chism (1971) and Bridge and Meredith (1983) reported that yield gains due to genetic improvement of cotton averaged 10.2 and 9.5 kg-ha<sup>-1</sup> per year since about 1910 in the United States. These yield advances have been accompanied by higher lint percentages, smaller seed bolls, and higher micromere values (Meredith and Wells, 1989). Wells and Meredith (1984) indicated that the major component contributing to increased yields was increase in number of fruits. This agrees with Evans's (1980) description of how yield was increased with smaller but more numerous fruits in other major crops.

Vandenberg and Nleya (1999) summarized traits that might optimize canopy structure in common bean at harvest and could be modified through breeding:

1. Long internodes in the lower stem
2. Consistent internode elongation under a wide range of environmental conditions
3. Reduction of stem stunting during early season growth
4. Increased stem length
5. Increased stem strength, particularly in the more basal internode
6. Reduction of pod length without decreasing seed size
7. Increase in pod curvature so that pod tips do not extend below the combine cutterbar
8. Long upright peduncles
9. Commencement of flowering at the upper nodes
10. High fertility at the upper nodes
11. Sufficient number of main stem nodes to maximize productivity in the available growing season

### *Cultural Practices*

In addition to breeding, plant architecture can be modified to a certain extent through cultural practices such as optimal plant spacing, plant density, and fertilization and water management. Miller, Hill, and Roberts (1991) noted that increasing stand density in lowland rice from 120 to 450 plants/m<sup>2</sup> linearly reduced the maximum tillers per plant from seven to three. The level of water management influenced plant survival and tiller appearance. Williams et al. (1990) found that established rice plant stands decreased with increasing water depth from shallow (2.5 to 7.5 cm) to moderate (10.2 to 15.2 cm) and deep (17.8 to 22.8 cm). Similarly, Fageria, Baligar, and Jones (1997) reported that application of N and P to upland, as well as lowland, rice increased tillering in central Brazil. Figure 1.6 shows yield increases of bread wheat as a function of year of cultivar release and N level.

Cultivars of cotton with reduced plant height, short branches, modified leaves, and combinations of these characteristics grown at high plant densities and in narrow-row systems could be a good alternative to increase yields of cotton (Reta-Sánchez and Fowler, 2002). Yield advantages of narrow rows was due to increases in light interception early in the season and increased boll production (Heitholt, Pettigrew, and Meredith, 1992).

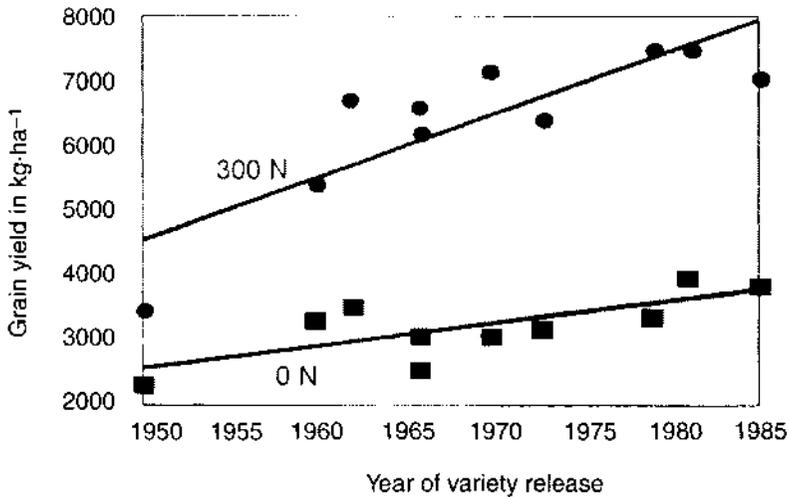


FIGURE 1.6. Grain yield of the historical series of bread wheats at Cd. Obregon, Mexico at 0 and 300 kg N·ha<sup>-1</sup>. Source: Braun, H. J., S. Rajaram, and M. V. Ginkel (1997). CIMMYT's approach to breeding for wide adaptation. In: P. M. A. Tigerstedt (ed.), *Adaptation in plant breeding* (pp. 197-205). Used with kind permission of Kluwer Academic Publishers.

Plant growth regulators such as cycocel (2-chloroethyl-trimethyl-ammonium chloride) are commercially used in Europe as an integral part of intensive cereal management systems to control lodging and maintain high yield potential (Batch, 1981). Khan and Spilde (1992) also reported reduced lodging and improved grain yields of wheat cultivars to ethephon (2-chloroethylphosphoric acid) (an ethylene-producing compound) application.

## CONCLUSION

Aboveground plant architecture and its components, including plant height, tillering or branching, leaf size, shape and arrangement, are important plant morphological characters related to yield. The main physiological function of the canopy is interception of light and subsequently plant photosynthetic activity. Distribution of leaf area within a plant canopy is a major factor determining total light

interception, which affects photosynthesis, transpiration, and dry matter accumulation. Vertical distribution of leaf area is determined by leaf size, leaf angle, and internodes length. Further, plant height is also related to plant lodging resistance, a character that determines plant yield capacity and grain quality. Some desirable plant architecture characters that are related to high yield are semi-dwarf plant height, thick, short, small and erect leaves, short and stiff culms, upright (compacted) tillering, high N response, and high grain-to-straw ratio. These characteristics can be modified through breeding and cultural practices. Plant breeders have developed high-yielding semi-dwarf cereal cultivars with stiff straw to reduce lodging potential. Complete elimination of lodging, however, has not been achieved without significant reduction in yield potential because of the close association between grain yield, plant height, and total biomass (Austin et al., 1980). High input responsive cultivars (water, fertilizers) of cereals and legumes, permit faster early growth and canopy closure, and reduce the time needed for an adequate root system to develop, thereby permitting the storage phase to begin earlier. Crop plant morphology has been modified to suit monoculture by reduction of branching in legumes or by more upright leaf inclination in cereals. The size of economic organs of plants has been increased substantially, and capacity of transporting assimilates to the various organs has also been increased through breeding during the past few decades (Evans, 1976).