# 11 Vegetative Growth

LEAVES supported by stems and branches are the carbohydrate factories of crop plants. They are necessary for the interception and transformation, via photosynthesis, of light energy to growth and yield. Leaves are also sources of nitrogen (N) for fruiting, mobilizing it and redistributing it to fruits.

Vegetative organs (including buds, leaves, and stems) have their origin in the apical and lateral buds of stems, starting with the embryo axis in the seed. Lateral or axillary buds are located in leaf axils. New growth can also arise from adventitious buds that may form in the stem cambium or the root pericycle.

Regardless of species or origin, buds are morphologically and functionally homologous (Fig. 11.1). They can conveniently be viewed as a series

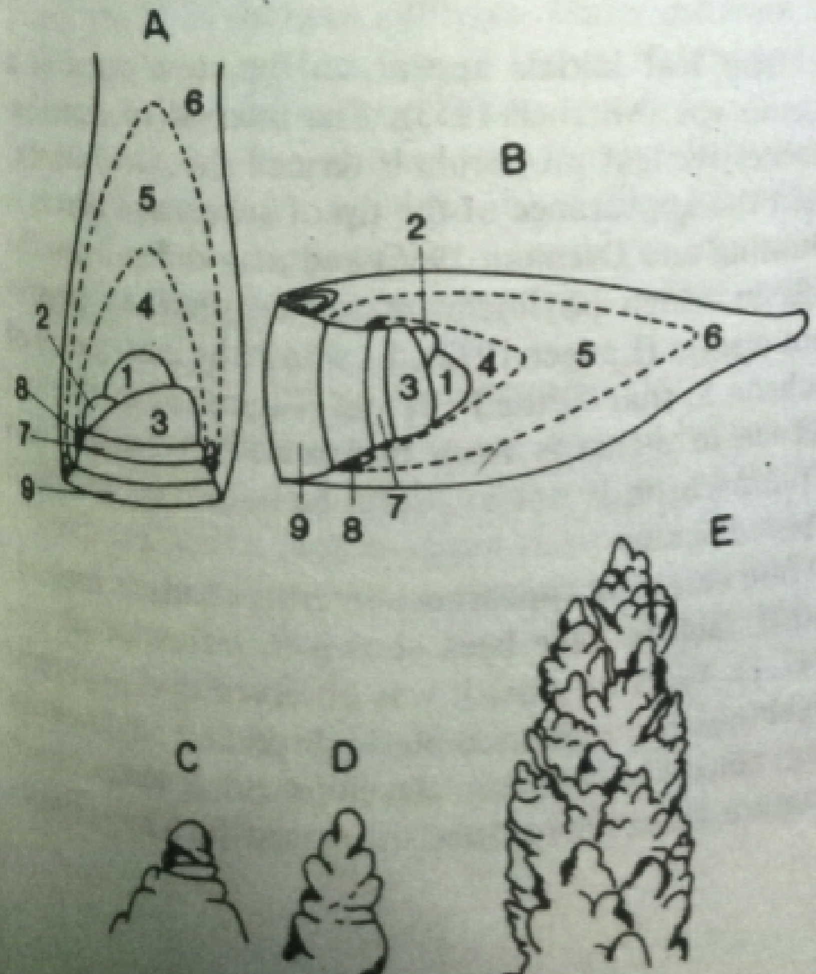


**Fig. 11.1.** Typical vegetative and floral buds of a grass plant. *A.* Bud of aerial stem or apical tiller. *B.* Apical bud of rhizome or rhizome branch. *C.* Vegetative shoot apex of oat. *D.* Inflorescence initial of oat at the 4-leaf stage. *E.* Inflorescence primordium of oat at the 6-leaf stage. Homomorphic structures in A and B: growing point (*1*), primordial leaves (*2* and *3*), expanding young leaves of an aerial shoot or expanding cataphylls of a rhizome (*4* and *5*), mature leaf sheath or rhizome cataphyll (*6*), unexpanded node and internode (*7*), axillary bud (*8*), and expanding internode of a rhizome (*9*) (aerial shoot internodes of temperate grasses do not elongate until after initiation of an inflorescence).

of structural subunits varying in degree of development from base to tip (*acropetally*). Each subunit of structure, the *phytomer*, has three components: (1) stem node and internode, (2) leaf, and (3) axillary bud. In some species more mature phytomers also have root initials. Phytomers develop acropetally and indeterminately. However, floral initiation terminates vegetative phytomers, as described above, and the components are modified as parts of the inflorescence. In temperate grasses, floral initiation also signals the beginning of stem (internode) elongation, which separates the leaves and elevates and exposes the inflorescence to a solar energy–rich environment at some height above the ground.

## Leaves

### INITIATION AND EMERGENCE

Leaf initials (*primordia*) begin with certain cells in the apical dome, which divide (become meristematic) and produce swellings or protuberances on the stem apex. The protuberances spread and encircle the apex, particularly the sheath primordium of a grass leaf (Fig. 11.1). After the leaf collar is formed, cells in the subhypodermis become meristematic and produce an axillary bud. Subsequent growth of leaf blades (*lamina*) and sheaths or petioles and stem internodes is from *intercalary* meristems (those between differentiated tissues).

In a grass leaf the intercalary meristem is divided into two parts by formation of the ligule. The upper part was found to contribute to lamina growth, the lower to the sheath (Jewiss 1966). Growth of a grass leaf occurs while the leaf is enclosed in the *pseudostem* (the rolls of older leaves). In dicots leaves emerge from short bud scales; therefore growth by expansion is principally in the open.

In a constant environment leaf initials appear on the stem apex at a constant rate for a given genotype (Mitchell 1953). The interval of time between the appearance of successive leaf primorida is termed the *plastochron*. The interval of time between the appearance of the tip of successive leaves is termed the *phyllochron* (Bunting and Drennan 1966) and may differ from the plastochron. Time intervals in which phyllochrons are longer than plastochrons result in longer shoot apexes (Langer 1972). In wheat the emergence of a given leaf tip is at plastochron 5; that is, the fifth leaf is initiated as the first leaf emerges. Since emergence in dicots is from bud scales, the distinction between phyllochron and plastochron is not as useful as in grasses in which leaf growth occurs in the pseudostem.

Research on leaf initiation rate and appearance in crop plants is limited. Temperature, light, and other factors have been shown to influence plastochron development (Table 11.1). With ryegrass it was observed that high temperatures (18–25°C) and light intensity increased plastochron and phyllochron rates. This is not surprising, since rate of plant development is temperature driven. Raising the temperature from 15 to 20°C increased leaf appearance

**TABLE 11.1. Rates of leaf appearance in perennial ryegrass**

| Temperature | Other Conditions | Rate (days • leaf$^{-1}$) |
|---|---|---|
| 25°C | ... | 5.8 |
| 18°C | 21,530 lx | 6.4 |
| 12°C | ... | 9.4 |
| 10°C | 21,530 lx | 10.0 |
| Winter | Unheated greenhouse | 15.5 |
| Winter | Heated greenhouse | 9.5 |

Source: R. H. M. Langer, *How Grasses Grow, Studies in Biology 34*, © 1979, by permission of Edward Arnold, Ltd.

rate in wheat by over 50% and shortened plastochron rate by 50%, from 5 or 6 days to 2 or 3 days (Langer 1972). Rate of leaf appearance in barley was linear as light increased from 7.8 to 32.5 W • m$^{-2}$ (Aspinall and Paleg 1963), but these effects could have been influenced by temperature changes.

## LEAF NUMBER

The number of leaves produced on a shoot or tiller is determined by inflorescence initiation. Formation of leaf initials on the apex gives way to floral initial formation (Fig. 11.1D) (Sharman 1945; Bunting and Drennan 1966), which fixes leaf number. Secondary and higher order tillers or branches generally have one to two fewer leaves than the primary shoot, since they emerge later and receive the same environmental cues to flower. Thus floral initiation is at a lower leaf number.

Characteristic leaf numbers are 7 to 9 for wheat, oats, and barley; 7 to 14 for sorghum; 14 to 21 for most U.S. maize hybrids; and 10 to 16 for upper-latitude U.S. soybean cultivars. Maize cultivars adapted from 50° latitude to the equator vary from 7 to 48 leaves. Height and maturity of maize are highly correlated to leaf number (Cross and Zuber 1973). The number of primordial leaves present in a mature seed embryo is characteristic of the species. Most cereal grains, such as wheat, have three leaves in the mature seed, while five leaves can be recognized in the embryos of maize seeds (Sass 1951). Plastochron 6 is during emergence or early seedling growth.

## FACTORS AFFECTING LEAF GROWTH

Leaf number and size are affected by genotype and environment (Humphries and Wheeler 1963). The position of the leaf on the plant (plastochron number), which is principally controlled by genotype, also has a pronounced effect on leaf growth rate, final dimensions (Bunting and Drennan 1966), and capacity to respond to improved environmental conditions, such as available water (Ralph 1982).

Leaf length, width, and area generally increase progressively with ontogeny up to a point; then in certain species these parameters decrease progressively with ontogeny so that the largest leaves are near the center of the plant,

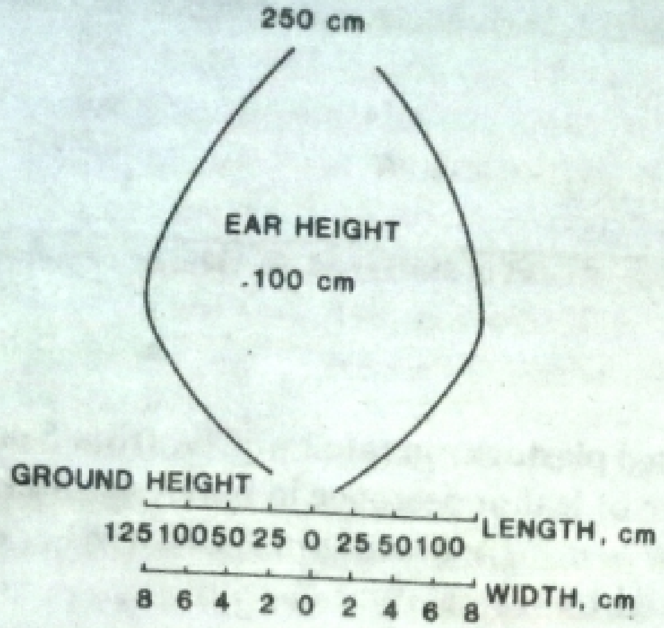


Fig. 11.2. Profile of leaf sizes of a maize plant.

such as on a maize plant (Fig. 11.2). The *flag* (uppermost) leaf of maize is shorter and narrower and has less area than the ear leaf. This type of profile is characteristic of many species. In other grasses, such as barley, the length of lamina decreased with flower initiation but the width increased, resulting in a broad flag leaf (Goodin 1972). The cause of the diminution of upper leaves is not known but appears to be competition with the inflorescence for nutrients. The relative growth rate of leaves decreases with leaf number (Milthorpe and Moorby 1974).

At stage 5 of soybean, 70% of the total plant dry weight was leaves (Hanway and Weber 1971). Leaf growth peaked at stage 6 and remained constant until stage 10, while total plant dry weight increased rapidly due to stem and fruit growth. Size and weight of new leaves decreased after stage 6; after stage 10 total leaf weight decreased due to senescence of bottom leaves. The maximum weight and area of the leaves of a plant is reached early in the life cycle, after which the gain in leaves just equals the loss, a status referred to as the critical leaf area.

Even though the lower leaves on plants are smaller and frequently lost due to environmental stresses and senescence, they are important to the vegetative growth. For example, $^{14}C$ fed to leaf 3 of a grass plant was active in leaf 4, 5, and 6 (Bunting and Drennan 1966). The lower pods of soybean were primarily supplied by the subtending leaves (Johnson et al. 1960). In barley the sheath plus stem contributed 50 to 70% as much of the apparent photosynthesis for grain production as did the blade (Thorne 1959). In dicots leaves with a long petiole and large petiole base make a significant photosynthetic contribution.

Nitrogen (N) fertilization had a pronounced effect on leaf expansion, especially on leaf width and area (Humphries and Wheeler 1963). With low N, leaf 4 of wheat was the largest in size; with high N, leaf 5 was largest. The shift in maximum size to an upper leaf was thought to have resulted from a reduc-