

## Stems

The stem consists of internodes spaced between the nodes, with attached leaves. The number of nodes and internodes is equal to the leaf number, all three having a common origin in the phytomer. Shoots of temperate grasses have compacted or untelescoped nodes (without internode elongation), which, until elongation after floral initiation, are positioned below the soil surface. At flowering, four to five of the upper internodes elongate and vertically space the upper leaves. A similar number of internodes remain short and compacted at or below the soil surface (referred to as the *crown*). Many dicot species are stemless until flowering. On the other hand, tropical species may produce vegetative stems, that is, internode growth without flowering.

Westmore and Steeves (1971) classified plants based on internode length as follows: (1) short stem (those without conspicuous internodes, such as plantains and the first-year growth of biennials) and (2) long stem (those with conspicuous internodes, such as maize and the second-year growth of biennials).

### INTERNODE ELONGATION

Growth in height of stem occurs in the intercalary meristems of the internodes (see Chap. 8). Internodes lengthen both by increases in cell number and (primarily) by cell expansion, the latter resulting in an increase of up to 25 cm or more. Growth by cell division is at the internode base (i.e., intercalary) rather than in apical meristems. However, intercalary meristematic activity is distributed throughout the length of the leaf lamina, sheath, and internode at the primordial stage (Fig. 11.4). With maturation, the meristem activity moves to the basal regions and eventually terminates (Sharman 1942).

The *peduncle* (internode supporting the inflorescence in grasses) and the flowering stalk (of dicots) grow from intercalary meristems. Generally internode growth is determinate for reasons not fully understood but apparently due to a limitation of the potential number of active cells. An exception is found in the *mesocotyl* (first internode in grasses) (Vanderhoef et al. 1979),

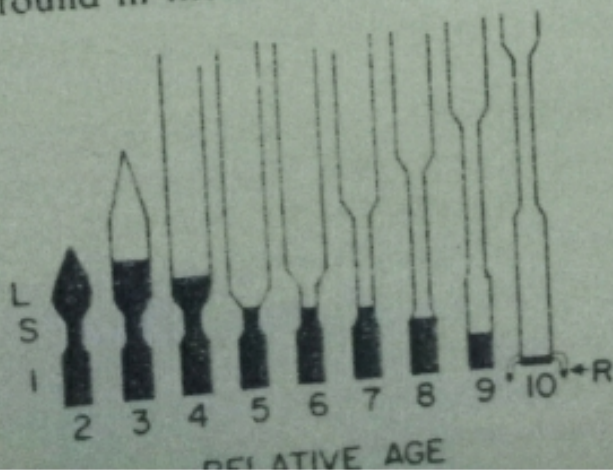


Fig. 11.4. Flux of intercalary meristematic activity (shaded) in relation to advancement of age of leaf stem tissue of a grass plant. Meristematic zone in leaf lamina (L), sheath (S), and internode (I) is reduced with time to a small area at the internode base and the tips of root initials (R). (From Sharman 1945. Reprinted by permission. © University of Chicago Press. All rights reserved.)

which, within food reserve limits, continued to elongate indefinitely in darkness or in infrared light. Growth of the mesocotyl is inhibited immediately by exposure to red light; that is, growth is phytochrome (pigment) controlled but modifiable by organic nutrition. In addition to growth limitation because of the number of active cells, the amount of growth hormones in the intercalary meristems may be limited since they are not self-generating as in apical meristems. Consequently plant growth regulators (PGRs) must be supplied from plant parts outside the meristem. Dwarf plants can respond to an exogenous (external) source, generally to gibberellin (GA) applications.

Maize remains stemless until reaching a height of about 40 cm and developing eight fully expanded leaves, which arise from the *pseudostem* (a vegetative shoot). At this stage there is no perceptible internode growth (Fig. 11.5). Due to compacted nodes and internodes, biennials produce a stemless rosette during the first year. Until flower initiation, temperate grasses produce pseudostems. At floral initiation the internodes of grass and biennial shoots that bear an inflorescence elongate. In early season a grass plant usually has both vegetative and reproductive tillers (*culms*).

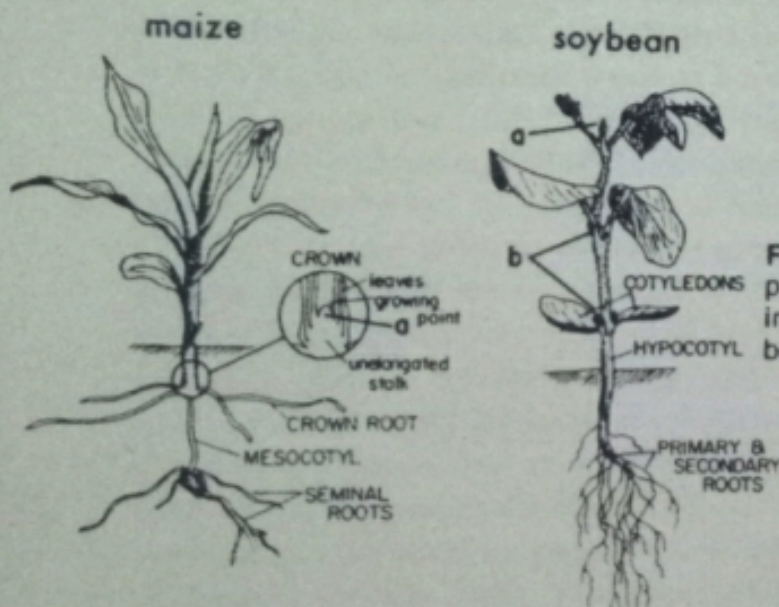


Fig. 11.5. Young maize and soybean plants showing position of apical growing points (a) and axillary buds of soybean (b). (From Crookston et al. 1976)

In dicots with no stems (e.g., *Plantago*) the last internode below the inflorescence greatly elongates to produce a flowering stalk (Sachs 1965). Long flowering stalks are evident in certain other species, such as white clover. The *gynophore* (peg) of peanut can be considered a nodeless fruiting stalk although its morphogenesis by originating from the flower differs somewhat from the typical flowering stalk. In monocots and dicots with long stems internode length generally increases acropetally, but patterns alternating long and short internodes are characteristic of some species. Basal internodes of many species may be short enough to escape observation, whereas the uppermost internodes, especially the peduncle of a grass culm, may exceed 25 cm. Normally

two or more internodes elongate simultaneously, but in sunflower a new internode does not initiate elongation until the preceding internode has completed it (Sachs 1965). Meristematic activity to cause elongation of internodes, except in the gynophore of peanut (Jacobs 1947), is concentrated at the basal end, as indicated by the presence of mitotic activity in stained cells.

### CROWN DEVELOPMENT

The lower, closely spaced nodes of a plant form the crown, which is located at or just below the soil surface. In grasses these densely spaced nodes give rise to the successive whorls of adventitious roots called the nodal, crown, or coronal root system (Fig. 11.5). The lower nodes of perennial legume plants such as alfalfa form a crown but without adventitious root development.

The location of growing points in the grass crown below the soil surface and resultant exposure of new leaves from sheaths of older leaves (pseudostem) have crop management implications. Since maize maintains this condition for 4 or more wk (until approximately eight leaves are fully exposed) (Fig. 11.5), an early frost or clipping usually injures only the above-ground foliage, the oldest and smallest leaves. Little permanent injury is caused by such early defoliation, since a new canopy of leaves soon emerges from the unspent intercalary meristems protected by the leaf roll and from newly formed leaves. The common practice of pasturing wheat during winter and early spring in the southern United States does not seriously damage grain production as long as the growing points of shoots remain vegetative, that is, below the soil surface. After floral initiation and concomitant stem elongation with the onset of longer spring days, grazing can remove the inflorescence and destroy the grain production potential. Unlike temperate grasses, dicots and many tropical grasses grow from exposed buds of aerial stems (Fig. 11.5, soybean). Hence, freezing or destruction of above-ground shoots can destroy axillary buds and regrowth potential. If a killing frost should occur on soybean, for example, growth potential is destroyed because no buds are present below the cotyledon axils, which are above ground; reseeding of the crop is necessary.

### FACTORS AFFECTING STEM GROWTH

**Growth Regulators.** The effect of plant growth regulators, especially GAs, on stem growth is well documented. They can overcome dwarfism in genetic dwarfs, such as dwarf maize and pea, promoting increased internode growth and normal height presumably by correcting an endogenous GA deficiency (see Chap. 7). However, the dwarf habit in dwarf 'RS 610' sorghum was not corrected by GA sprays; only the below-ground nodes (mesocotyl and second internode) and the coleoptile responded (Gardner and Kasperbauer 1961). This comparative lack of response in sorghum was probably due to the fact that sorghum dwarfing is controlled by several genes, and maize and pea dwarfing by a single gene (Windscheffel et al. 1973). Evidently GA is more effective in correcting dwarfing that is inherited simply.

Leopold (1949) showed that auxin has a pronounced effect on *tillering* (growth of shoots from crown buds) in barley (Table 11.2). When the shoot apex and source of auxin was destroyed, 'Wintex' barley tillered profusely unless given an application of the auxin naphthaleneacetic acid (NAA). The NAA-treated plants with destroyed apices tillered about the same as normal plants, that is, those with undisturbed apices.

**Light.** Light has a pronounced effect on stem growth. In the dark, *etiolation* (elongation of internodes) is extreme and similar to that of the mesocotyl internode. The internodes of shaded plants, such as in dense stands, are more etiolated. The shade effect is believed to be due to auxin enhancement, probably acting synergistically with GA. Theoretically photodestruction of auxin is less in shaded stands, since high irradiance decreases auxin and plant height.

Day length affects stem growth usually less conspicuously than it affects flowering. Consequently photoperiodic responses of stem development are not often reported. Long days cause increases in internode length and plant height, especially on short-day plants. Soybean cultivars adapted to northern latitudes had fewer and shorter internodes and flowered earlier when grown at lower latitudes (Shibles et al. 1975). Planting the same cultivars at higher latitudes than those to which they are adapted has the reverse effect and would also probably result in immature seeds at harvest. Much earlier seeding dates in an area of adaptation tend to result in the same response as to shorter days characteristic of lower latitudes. For example, early planting produces shorter internodes in maize, which results in sturdier plants.

As with leaf growth, internode growth of grasses is influenced by light quality. Both grow from intercalary meristems of common origin and are shielded from light in the roles of older leaf sheaths, producing a dark or far-red effect (Fig. 11.5). Far-red light (maximum effectiveness at 730 nm) promotes, and red light (maximum effectiveness at 660 nm) inhibits, mesocotyl elongation (Vanderhoef et al. 1979), the mechanism controlling emergence from variable planting depths. In wheat, emergence is primarily from elongation of the second rather than the first internode or mesocotyl; distinct effects of monochromatic light on upper internodes has not been demonstrated. However, in grasses these internodes and young leaves are trapped in the darkness of the sheaths of older leaves for the greatest part of their total growth. Consequently the phytochrome-far-red response appears to be operative. Growth is inhibited when exposed to light.

Dicot internodes are not so enclosed in leaf rolls, probably indicating little or no phytochrome-monochromatic light response, but this relationship has not been well established. However, a bush-type garden bean under long night-far-red radiation (see Chap. 12) in effect assumed a climbing habit (internode elongation) due to development of long internodes (Kretschmer et al. 1977), a single-gene response. Flowering, which was independent of the

climbing habit, was promoted by short nights (long photoperiods). It was concluded that flowering response and climbing habit are both phytochrome controlled but are discrete, independently inherited responses.

Mineral nutrient and water availability affect internode growth, especially by cell enlargement, as in any vegetative or fruiting organ. Nitrogen and water, particularly, increase plant height, but the effect is complex since a larger leaf size results in more shading. Shading tends to increase auxin levels, which could affect internode length.

## Branching

Whether buds in leaf axils resume growth to produce side branches (e.g., in dicots) or tillers in grasses depends on genotype and environment. The potential for axillary branches is always present, since there is a bud in each leaf axil. Modern maize hybrids do not tiller, except for the development of ear shoots, despite favorable environments because of strong internal (genetic) control (Duncan 1975). Ear shoots can be forced to develop at several lower nodes if apical dominance is broken. For example, removal of a young ear shoot on a maize plant stimulates development of the next lower ear. The potential number of ears is equal to leaf number, since axillary buds and leaves are phytomer components. The number of shoots that actually develop on grass plants is always less than the potential, due to genetic and environmental controls.

Three types of tillers of grasses have been described by Arber (1934):

1. Upward, or *apogeotropic*. These tillers are similar in appearance to the primary shoot but have one or two fewer leaves and often remain vegetative even though the primary shoot and even sister tillers are reproductive. These *intravaginal* tillers emerge from live leaf sheaths (Fig. 11.6).

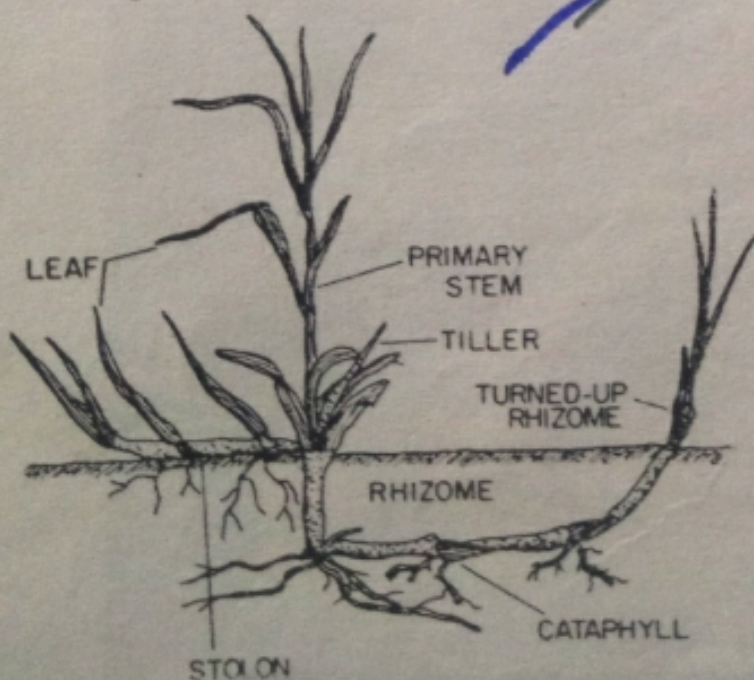


Fig. 11.6. Branching habit of a perennial grass plant, showing the main shoot in relation to the axillary branches: stolon, aerial tiller (intravaginal), and rhizome (with cataphyll) turned up to produce a new primary shoot.

2. Horizontal, or *diageotropic*. Stolons and rhizomes belong to this type. They differ from upright shoots in certain morphological details. Generally, rhizome and stolons emerge from dead sheaths of the most basal nodes at or below the soil surface. Stolons grow horizontally above ground and produce normal stems and leaves (Fig. 11.6). Rhizomes grow below ground and produce modified leaves without laminae (*cataphylls*), on stems that have normal nodes and internodes (Fig. 11.6).

3. Downward, or *geotropic*. These stem types are not common in occurrence.

### TILLERING

Upward, or intravaginal, axillary shoots in grasses are commonly referred to as *tillers*. Shoots from axillary buds on stems of dicots are usually referred to as side branches. Their origin and development morphogenetically are the same: both emerge from leaf axils, generally from the lower nodes, if the shoot is not apically dominant. Tillers emerge acropetally, beginning at the lowest nodes. In wheat the first tiller emerges from the coleoptile axil, in rice from the leaf-3 axil (Murata and Matsushima 1975). Regardless of species, the lower leaf axils of the main stem give rise to the primary tillers. These in turn give rise to the secondary tillers, which give rise to the tertiary tillers, and so on. In general all primary tillers emerge before any secondary and tertiary tillers. Perennial grasses tiller throughout the season. This tillering habit, along with accumulation of food reserves, is the primary basis for *perennation* (living from season to season). Rice and sorghum, temperate annuals, have these characteristics and perennate in tropical climates. This perennial habit of rice and sorghum is often exploited in tropical areas to produce *ratoon crops* (regrowth from stubble).

Tiller production in cool-season perennial grasses is subject to wide seasonal fluxes. In 'S 170' tall fescue tillering increased exponentially during spring, was static during summer, and increased again during autumn, accumulating a total of 300 tillers per plant (Robinson 1968). In March of the following year the number declined to 250, in June to 100. The tillering habit in timothy is much weaker than in tall fescue, as is the capacity to perennate and persist. Temperate grasses produce large numbers of reproductive tillers in spring to early summer. They also produce an equal or greater number of vegetative tillers then and produce only vegetative tillers later in the season. The vegetative tillers produce leaf growth during the growing season, overwinter, and become reproductive tillers the next season, having been vernalized by the cool temperatures and short days of the previous fall (Gardner and Loomis 1953). Tropical grasses generally produce vegetative stems with distinct nodes and internodes as tillers. Their vegetative and reproductive tillers are similar in appearance prior to panicle emergence. Reed canarygrass, although temperate, often produces vegetative aerial stems. Dallas and bahiagrass (*Paspalum*

The tillers arise as axillary buds on the stem apex as a result of meristematic activity in subhypodermal tissue. In the embryo of the seed, buds are usually viable in the axil of the coleoptile and the first one or two foliage leaves. After germ<sup>n</sup> new buds are initiated at the same rate as primordia. Buds are thus laid down in regular succession from the base upwards, or acropetally as it is called, and they tend to emerge as tillers in the same order. Each bud is the replica of the parent structure, complete with apical meristem, leaf primordia and axillary buds. On emergence the tiller again resembles the parent shoot with its own system of leaves attached to a highly contracted stem and its own adventitious roots. Although complete in every respect, tillers remain in vascular connection with one another.

A tiller emerges from the encircling leaf sheath in one of two ways, depending on the species. In tufted grasses the tiller grows upwards within the sheath and first appear externally near the base of the parent lamina.

Alternatively, a tiller may break through the protecting sheath and give rise to a stolon as in meadow grass which is rough-stalked or a rhizome as in couch. However, at the nodes of their creeping stems these species may produce plants with a tufted growth habit within which the former type of tillering occurs. Whichever the mode of emergence, it depends on the genotype and environmental conditions whether or not a bud develops into a tiller.

Factors affecting Tillering.

The amount of tillering is genetically controlled. Some species produce tillers freely, and indeed pasture grasses are often selected for this characteristic, while others tiller only sparsely. However, although genotypic differences exist, tillering is highly modified by the environment.

✓ in wheat 1st tiller from axillary bud  
in rice 3rd leaf node

(2)

### The effect of temp.

In wheat a rise of temp. from 10-25°C<sup>o</sup> was found to favour leaf production more than tillering. The inhibitory effect of high temp. appears to be related to resp<sup>n</sup> rates and the soluble-CHO content of the plant, since warm conditions at night are often more deleterious than during the day.

### Mineral nutrition.

Tiller production is greatly increased by raising supply of nitrogen, Phosphours and potassium and limitation of other essential elements would also be expected to have an effect. It is because tillering implies intense meristemati activity and cell enlargement.

### Growth regulators.

Triiodo~~xy~~benzoic acid (TIBA) is known to inhibit auxin transport, and stimulates tiller bud growth. Similar effects have been obtained with Kinetin in wheat, while Gibberellins usually de~~press~~ tillering. The general pattern to emerge from these experiments is that internal competition for metabolites <sup>avoids</sup> ~~provably~~ limits tiller bud growth, and that growth substances may well regulate the activity of competing sinks.

### Maturity

The word mature is ordinarily used to refer to a state of development which is capable of flowering, in some species this capability is achieved only gradually, e.g., the increasing flowering of citrus with age. Maturation, then, is achieved through a gradual transition of morphology, growth rate, and flowering capacity. Some characteristics that change between the juvenile, mature, and senescent stages are fairly stable and only slightly altered by graftage of buds onto trees of another developmental stage; e.g., the juvenile leaf form