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GENERAL DESCRIPTION OF GRASS GROWTH DEVELOPMENT

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Plant developmental morphology is the study of plant growth and development. Grassland managers need a working knowledge of grass growth and development in order to understand when to apply specific management practices, to know the effects of various management practices on plant communities, and to be able to anticipate the secondary effects on livestock and wildlife.

Grass plants consist of shoots and roots. Shoot is a collective term that applies to the stem and leaves. The shoot is made up of repeated structural units called phytomers (Beard 1973, Dahl 1995), each comprising four parts: 1) a leaf, consisting of a blade and sheath, with a collar separating the two structures; 2) a node, the location of leaf attachment to the stem; 3) an internode, the length of stem between two successive nodes, and 4) an axillary bud, the concentration of meristematic tissue capable of developing into a tiller (Hyder 1974, Dahl and Hyder 1977). Meristematic tissue is a collection of undifferentiated cells concentrated in growth point areas called meristem. Each shoot generally has 5 or 6 phytomers but may have 7 or more. Collectively the nodes and internodes of the phytomers are called the stem. The vegetative stem consists of a few to several nodes and unelongated internodes, with the apical meristem located at the highest node, at the top (apex) of the stem (Langer 1972). The crown of a grass plant is the lower portion of a shoot and has 2 or more nodes (Dahl 1995).

Plant growth, a quantitative change in plant size (Dahl 1995), occurs through an increase in the number of cells by cell division in meristematic tissue and through cell enlargement and elongation. Most new cells are produced in the apical meristem. In species with short shoots the apical meristem remains near ground level; in species with long shoots the apical meristem is elevated before its status changes from vegetative to sexually reproductive (Dahl 1995).

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New cells in the apical meristem form growth centers and develop into leaf primordia (leaf cells in their earliest stage of differentiation), which develop into phytomers. Almost all of the cells of the leaf are formed while the leaf is a minute bud (Langer 1972). Elongation of cells and differentiation of cell masses into various tissue types begin at the tip of the leaf (Langer 1972). The oldest cells of a leaf are at the tip, and the youngest cells are at the base (Langer 1972, Dahl 1995).

Leaf bud primordia are formed on alternating sides of the apical meristem (Evans and Grover 1940, Langer 1972, Beard 1973, Dahl 1995). Several leaf primordia are at various stages of development at any one time. The oldest leaf is outermost while younger leaves grow up through existing leaf sheaths (Rechenthin 1956, Beard 1973). Growth of the leaf results from an expansion in cell size (Esau 1960, Dahl 1995), occurring in the region protected by the sheaths of older leaves. When the cells emerge and are exposed to light, expansion ceases and photosynthesis (the process which occurs in the presence of light and by which plants take carbon dioxide from the air, build carbohydrates, and emit oxygen) and transpiration (emission of gases through the leaf pores) begin (Langer 1972). The new growing leaf receives carbohydrates from roots, stems, or older leaves until its growth requirements can be met by the leaf assimilates (a complex of constituents that are the end products of the photosynthetic process).

A few leaf cells are produced by meristematic tissue separated from the apical meristem. These areas are called intercalary meristem and are located at the base of the blade, the base of the sheath, and the base of the internode (Esau 1960). The leaf intercalary meristems remain in basal positions, a morphological (structural) feature that contributes to the grazing tolerance of grass plants by permitting the elevated part of the leaf blade to be removed without an accompanying cessation of growth. Intercalary meristems of leaf blades cease activity by the time the leaf collar is exposed. Once a leaf blade is fully expanded, no further growth of that blade is possible (Dahl 1995).

Individual leaves of grass plants are relatively short lived. Young middle-aged leaves are in their prime when the rate of apparent photosynthesis is maximum and the leaves begin exporting assimilates to other parts (Langer 1972). At this point the leaf has its greatest dry weight. Leaf senescence, or aging, begins shortly after middle age. Senescence begins at the tip, the oldest part of the leaf, and spreads downward. As senescence progresses, apparent photosynthesis decreases and movement of assimilates from the leaf to other parts of the plant ceases (Langer 1972). The rate of senescence is influenced by environmental conditions but occurs at about the same rate as leaf appearance. During senescence, cell constituents are mobilized and redistributed to other parts of the plant

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(Beard 1973). This process causes weight of the leaf to decrease (Leopold and Kriedemann 1975). The percentage of dryness in a leaf blade is an indicator of the degree of senescence. Drying leaves are probably neither an asset nor a detriment to the plant.

Roots grow from the nodes that are in the crown and are on or below the ground. The internodes located in the crown and associated with roots and rhizomes do not elongate (Dahl 1995). Adventitious roots (secondary roots developing from the stem rather than from root tissue) form in tissue at the nodes just below the internodal intercalary meristem (Langer 1972). It appears that all roots have a limited life span, probably little more than a year at most. Within the root system turnover of root material is continuous, involving senescence, death, decay, and new formation.

Grass plants reproduce by two processes, asexual reproduction and sexual reproduction, which correspond to vegetative and reproductive phases, respectively. The dates for initiation of vegetative growth for perennial graminoids are variable with species and local environmental factors, primarily temperature and photoperiod (length of daylight) (Langer 1972, Dahl 1995), and also precipitation (McMillan 1957, Trlica 1977). Vegetative shoots develop from a main shoot by the process of tillering. A tiller is a shoot derived from vertical growth of an axillary bud (Dahl 1995) and is a complete unit with roots, stem, and leaves. There are two types of tillering: intravaginal and extravaginal. Intravaginal tillers grow vertically, close to the main shoot and within the enveloping leaf sheath, and tend to have a tufted or bunch-type growth habit (Dahl and Hyder 1977, Dahl 1995). Extravaginal tillers penetrate the enveloping sheath and grow horizontally away from the main shoot for a distance before vertical growth. This type of tillering results in the spreading or creeping growth habit of sod-forming plants (Dahl and Hyder 1977, Dahl 1995). If this horizontal growth is below the soil surface, it is called a rhizome (Beard 1973), and if it is aboveground it is called a stolon (Dahl 1995). Rhizomes may be either continuous, producing tillers at progressive intervals, or terminal, producing 1 tiller when the apex turns up and emerges from the soil (Dahl 1995). Stolons have continuous growth and form tillers at progressive nodes (Dahl 1995). Early vegetative growth is dependent on carbohydrates stored in the roots, rhizomes, or stem bases (Trlica 1977). All young tillers are dependent on the main shoot for carbohydrates until they have developed their own root systems and mature leaves (Dahl 1995). After the tiller becomes independent it remains connected to other tillers by vascular tissues (xylem and phloem used in conducting water, mineral salts, and synthesized food) (Moser 1977, Dahl and Hyder 1977, Dahl 1995).

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Reproductive growth can begin after the plant has met a certain minimum amount of vegetative development (Dahl 1995). The status of the apical meristem changes from vegetative to reproductive between the 3.0 and 3.5 leaf stage (Frank 1996, Frank et al. 1997); flower bud primordia develop on the apical meristem, formation of new leaf primordia is inhibited, and no more leaf primordia can be laid down (Esau 1960, Langer 1972). The flower bud primordia (flower cells in their earliest stage of differentiation) develop into the inflorescence (the flower-and-seed-bearing portion of the stalk), with the apical dome becoming the terminal (top) spikelet. Inflorescence initiation cannot be detected without destruction of the plant, but shortly after initiation the developing inflorescence enlarges, and swelling of the enclosing sheath, the first external evidence of stalk development, is noticeable. This stage of flower stalk development is occasionally referred to as the "boot" stage. At this point, 4 or 5 upper internodes along with the attached leaf sheaths elongate very rapidly. This short phenophase (an identifiable growth stage related to climate and/or time of the year) is referred to as head emergence phenophase. The inflorescence reaches near-maximum height shortly after emergence, and flowering and fertilization soon follow.

The reproductive phase is triggered primarily by photoperiod (Roberts 1939, Leopold and Kriedemann 1975, Dahl 1995) but can be slightly modified by temperature and precipitation. Some plants are long-day plants and others are short-day plants. The long-day plants reach flowering phenological stage after exposure to a critical photoperiod and during the period of increasing daylight between mid April and mid June. Generally, most cool-season plants with the C_3 photosynthetic pathway are long-day plants and reach flower phenophase before 21 June. The short-day plants are induced into flowering by day lengths that are shorter than a critical length and that occur during the period of decreasing day length after mid June. Short-day plants are technically responding to the increase in the length of the night period rather than to the decrease in day length (Weier et al. 1974, Leopold and Kriedemann 1975). Generally, most warm-season plants with the C_4 photosynthetic pathway are short-day plants and reach flower phenophase after 21 June. The annual pattern in the change in daylight duration follows the calendar and is the same every year for each region.

Plant populations persist through both asexual (vegetative) reproduction and sexual reproduction (Briske and Richards 1995). The frequency of true seedlings is low in established grasslands and occurs only during years with favorable moisture and temperature conditions (Wilson and Briske 1979, Briske and Richards 1995), in areas of reduced competition from older tillers, and when resources are easily available to the growing seedling. Sexual reproduction is necessary for a population to maintain the genetic diversity enabling it to withstand large-scale

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changes (Briske and Richards 1995). However, production of viable seed each year is not necessary to the perpetuation of a healthy grassland. Reproductive shoots are adapted for seed production rather than for tolerance to defoliation (Hyder 1972). Grass species that produce a high proportion of reproductive shoots are less resistant to grazing than are those species in which a high proportion of the shoots remains vegetative (Branson 1953). Vegetative growth is the dominant form of reproduction in semiarid and mesic grasslands (Belsky 1992), including the tallgrass, midgrass, and shortgrass prairies of North America (Briske and Richards 1995).

Successful management of grassland ecosystems requires knowledge of grass growth and phenological development of grasses within a geographic region. Management strategies based on phenological growth stages of the major grasses can be planned by calendar date after the relationships between phenological stage growth of the major grasses and time of season have been determined with consideration of a possible variation of about $\pm$7 days to accommodate annual potential modification from temperature and precipitation (Manske 1980). Implementation of such strategies has the potential to maintain stability of the grassland ecosystem and allow sustained livestock production.

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